# POPULATION CONNECTIVITY AND ITS APPLICATION TO MARINE PROTECTED AREA EFFECTIVENESS IN A SUB-ARCTIC COASTAL ECOSYSTEM

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# Population Connectivity and its Application to Marine Protected Area Effectiveness in a sub-Arctic Coastal Ecosystem

by

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**Abstract**

Atlantic cod (*Gadus morhua*) in Gilbert Bay provides an opportunity to better understand the potential effectiveness of a Marine Protected Area (MPA) in providing protection for a specific population, including the roles that oceanography and behaviour may play in population connectivity. This thesis uses long-term monitoring and research (1998-2011) through mark-recapture tagging, oceanographic sampling, ichthyoplankton tows, and acoustic telemetry tracking to describe demographic trends and population connectivity of the Gilbert Bay Atlantic cod population in southeastern Labrador, Canada. The population declined considerably after Gilbert Bay became a MPA, presumably as a direct result of legal fishing activities outside MPA boundaries. Therefore connectivity research was undertaken to investigate population dynamics and infer strategies to improve MPA effectiveness. The locally adapted timing and location of spawning strongly influences the population's localized connectivity, resulting in egg retention at the spawning area. Tagging showed high site fidelity in juvenile and adult cod and that migratory adults exhibit strong homing behavior. Migratory adults move up to 40 km from the population's core area, but return to that core area to overwinter and spawn. Transplant experiments demonstrated the importance of prior experience for successful homing. Fish displaced outside their known or assumed home range displayed very low homing success compared to those displaced to areas within their home range. Adolescent and adult Atlantic cod migrated briefly from the head of the bay towards coastal areas for summer feeding, which increased susceptibility to fishing in areas outside the MPA. However, most ultrasonically tagged fish moved less than 10 km

outside MPA boundaries. This new information on the timing and locations of fish movement can improve MPA effectiveness by identifying times and locations when a portion of the protected population moves away from the MPA and becomes vulnerable. Such knowledge can facilitate adaptive management and improved co-operation between MPA stakeholders and fisheries managers.

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## Table of Contents

## List of Tables

Tables Page

## List of Figures

List of Appendices

## Co-Authorship Statement

The research described in this thesis were designed and conceptualized by C.J. Morris, with assistance from J. M. Green. Paul Snelgrove provided assistance with thesis preparation, writing, and presentation of data. C. J. Morris was responsible for all data collection and analyses, in collaboration with Dr. John Green. All manuscripts resulting from this thesis work were prepared by C. J. Morris, with editing assistance and creative input from J.M. Green and Paul Snelgrove.

## Chapter One

## General Introduction

Population connectivity refers to the exchange of individuals among subpopulations (Cowen et al. 2006), and marine population connectivity research over the past decade has changed ecological understanding of marine populations from a common view of broad dispersal and homogenous population structure to one that recognizes that discrete populations are much more common than previously thought (Thorrold et al. 2001; Warner and Cowen 2002; Kinlan and Gaines 2003; Shanks et al. 2003; Cowen et al. 2006; Cowan et al. 2007; Jones and Srinivasan 2007; Pineda et al. 2007). Increasingly studies report intraspecific differences among genetic attributes, growth rates, reproductive characteristics, population size, and behaviour, often at smaller scales than previously recognized (Conover and Present 1990; Foster and Endler 1999; Jobling 2002; Jonsdottir et al. 2002; Berg and Albert 2003; Knutsen et al. 2007; Knutsen et al. 2011). These biological characteristics have significant potential to influence local adaptation (Felenstein 1976, Endler 1977; Olsen et al. 2008; Clarke et al. 2010).

Connectivity of populations defines and determines gene flow among them (Slatkin 1987; Ruzzante et al. 2006; Bradbury et al. 2012 and references therein). Biotic and biophysical factors that limit dispersal, such as local retention (Swearer et al. 1999), differential survival (Buston et al. 2011), reproductive success of migrants (Hendry and Taylor 2004; Nosil et al. 2005), and natal homing (Jones et al. 1999; 2005), can restrict gene flow and lead to fine-scale genetic structure (Jorde et al. 2007; Ciannelli et al. 2010) and local adaptation (Conover and Present 1990, Bricelj et al. 2005, Marcil et al. 2006; Olsen et al.

2008; Clarke et al. 2010). Over the last five decades, however, researchers have been debating the level of gene flow necessary to constrain evolution in the wild (Conover et al. 2006). Several authors contend that gene flow homogenizes populations and can negate local differences resulting from selection (Slatkin 1987; Hendry et al. 2002; Palumbi 2003), whereas others argue that natural selection typically overwhelms gene flow in nature so local adaptation can occur even with high gene flow (Erhlich and Raven 1969; Hedgecock et al. 2007; Marshall et al. 2010). Regardless, conserving and sustaining resources and healthy ecosystems for future generations requires recognition and understanding of the mechanisms that support biocomplexity (Hilborn et al. 2003; Schindler et al. 2010). Biocomplexity in this context refers to geographic population structure at different spatial scales and several dimensions of life history variation within this geographic structure (Hilborn et al. 2003).

Applied ecological research requires understanding of connectivity and local adaptation in order to improve conservation techniques that can sustain natural resources more effectively (Cowen et al. 2006; Clarke et al. 2010). The potential depletion of populations under a broadly applied management plan can lead to overall reductions in species resilience, intraspecific biocomplexity, and ecosystem health (Hilborn et al. 2003; Worm et al. 2006; Schindler et al. 2010). To conserve local populations, management effort needs to be applied at smaller scales than has traditionally been the case, adding additional challenges in understanding those smaller scales and developing management strategies appropriate to them. Large-scale global declines in marine resources over recent decades has re-focused applied ecology on the conservation and sustainability of

natural resources (Jackson et al. 2001; Jackson 2008; Worm et al. 2009; Tyus 2012). Some researchers maintain that improving existing harvest control rules can improve sustainability of resources (e.g., Hilborn et al. 2003), while others suggest a need for more dramatic changes in resource management (e.g., Worm et al. 2009). Some researchers embrace the application of Marine Protected Areas (MPAs) as a conservation tool in ecosystem and fisheries management (Botsford et al. 2009). MPA efficacy depends partly on the relationship between the MPA (its size, location and specific restrictions) and population connectivity. In particular, consideration of larval dispersal, juvenile and adult movements, and the activities of fishermen can greatly improve MPA effectiveness (Gaines and Gaylor 2007; Botsford et al. 2009) and MPAs should be considered on a case by case basis (Hilborn et al. 2003).

Atlantic cod offer a compelling model species for population connectivity in that their distribution spans both sides of the Atlantic Ocean (Scott and Scott 1988; Rose 2007) but nonetheless displays complex population structure (Brander 1994; Ruzzante et al. 2000; Beecham et al. 2002). Populations are capable of reaching levels of abundance in the millions (Rose 2007 and references therein), but discrete, persistent Atlantic cod populations specific to a bay, fjord, or offshore area characterize the species throughout its range (Templeman 1974; Ames et al. 1997; Taggart 1997; Knutsen et al. 2003; Robichaud and Rose 2004). A wide environmental tolerance range, behavioural flexibility, and local adaptation all likely contribute to their diversity and ecological success (Righton et al. 2010). Several studies report retention of eggs and larvae to specific areas, as well as homing behaviour, among Atlantic cod populations (Knutsen et

al. 2003; Svedang et al. 2007; Ciannelli et al. 2010; Knickle and Rose 2010). All of these elements of Atlantic cod behaviour may be important in identifying the relevant scales and factors affecting population connectivity.

Commercial exploitation of Atlantic cod, and in particular the northern cod stock (NAFO Divisions 2J+3KL), yielded remarkable catches in terms of numbers of individuals harvested but fishing effort ultimately resulted in stock collapse in the late 1980's and early 1990's (Steele et al. 1992; Lear and Parsons 1993; Rose 2007). The northern cod stock, described as a stock-complex with several populations (Smedbol and Wroblewski 2002), is managed as a single unit within NAFO Subdivisions 2J3KL (Halliday and Pinhorn 1990). Managing easily fished, semi-independent populations to prevent overexploitation or elimination represents perhaps the single most difficult management problem for exploited populations such as inshore northern cod (Myers et al. 1997 and references therein). The absence of a recovery in this stock since its collapse in the early 1990's (DFO 2012) has become a global example of the importance of fisheries management (Hutchings 2000, 2004), and an example of the need for better knowledge of population structure and connectivity (Stephenson 1999; Sterner et al. 2007; Reiss et al. 2009). For example, Ames (2004) suggested that fishing depleted local inshore population components of Atlantic cod in the Gulf of Maine. Similarly, Myers et al. (1997) raised concern over the overexploitation of inshore northern cod populations.

Gilbert Bay, Labrador supports a local Atlantic cod population within the northern cod management area (Green and Wroblewski 2000; Morris and Green 2002). Biological

characteristics of this population were described previously (Morris and Green 2002) and genetically it is considered an island of genomic divergence (Bradbury et al. 2012). As populations diverge, elevated differentiation of genomic regions associated with adaptation often result in heterogeneous genomic divergence. Geographic differentiation in Atlantic cod appears to be driven by a small number of discrete islands of genomic divergence (Bradbury et al. 2012). Gilbert Bay cod comprise the most discrete Atlantic cod population among those investigated in the western Atlantic (Ruzzante et al. 2000; Beacham et al. 2002; Bradbury et al. 2010), with the exception of relict Atlantic cod populations inhabiting meromictic lakes on Baffin Island (Hardie et al. 2006). Gilbert Bay was formally designated a Marine Protected Area (MPA) by Canada's Oceans Act in 2005 (Canada Gazette, 2005). The specific regulatory intent of the MPA is to protect the local Gilbert Bay cod population and its habitat.

This thesis addresses changes in the Gilbert Bay cod population based on long-term monitoring and research (1998-2011) and considers the contribution of population connectivity to MPA efficacy. Chapter 2 identifies a worrisome decline in abundance and changes in population structure over a 14-year monitoring period as a direct result of fishing pressure and variable recruitment. Chapter 3 investigates the retention of Atlantic cod eggs and larvae in Gilbert Bay, and emphasizes the importance of bathymetry and oceanographic conditions in relation to timing and location of cod spawning for connectivity of this population. Chapter 4 evaluates the movement patterns of juvenile and adult Gilbert Bay cod. Armed with specific knowledge of the population's home range and movement patterns, transplant experiments demonstrated the importance of

individual experience for Gilbert Bay cod homing behaviour. Chapter 5 presents evidence of seasonal migration over small spatial scales to feed in more productive coastal areas. Chapter 6 presents details of cod movements to areas outside the MPA and proposes how scientific information can advise potential adaptive management actions that could improve effectiveness of the Gilbert Bay MPA. Chapter 7 concludes on how improved understanding of connectivity, coupled with long- term monitoring and research represent critical scientific inputs to advise managers on how to improve MPA design and effectiveness for threatened populations. Specifically, it identifies how changing the timing of fishing closures in adjacent areas can allow protected fish to complete their feeding migration without risking capture in commercial fisheries and without further limiting fishing opportunities to local fishers.

## Chapter Two

## Long-term Atlantic cod population trends in a subarctic MPA: How connectivity research can improve MPA efficacy

### 2.1 ABSTRACT

Gilbert Bay, Labrador was closed to commercial fishing for Atlantic cod (*Gadus morhua*) in 2000, and became a Marine Protected Area (MPA) in 2005 regulated under Canada's Fisheries Act and Oceans Act, specifically to protect the genetically distinct population of Atlantic cod and its habitat. Population monitoring and research conducted in Gilbert Bay during 26 research trips and over 14 years of sampling have shown major population changes, resulting from variable recruitment and commercial fishing pressure in areas adjacent to the MPA. The pattern of juvenile recruitment of fish has included several strong year classes followed by several poor year classes throughout the period. Tag recaptures from the commercial fishery (n=105) indicate that commercial fishing activities removed some large adult Gilbert Bay cod that migrated outside the MPA. Relatively intense commercial fishing in the time series available, during a period of poor recruitment, correlated with a declining trend in research catch rates, and truncated size structure. The large changes in population abundance indicate a need for adaptive management in order to improve MPA effectiveness.

## 2.2 INTRODUCTION

Many ecologists consider Marine Protected Areas (MPAs) to be an important conservation and management tool for marine ecosystems (CBD 2006). Many MPAs have been established throughout the world's oceans (Botsford et al. 2009) each with various objectives. MPAs vary in design and application, but most restrict at least some activities from a specific area to reduce unwanted effects or to enhance specific ecological attributes, sometimes hoping for a positive spillover effect on larger, adjacent areas. MPAs established specifically to protect fish populations are typically expected to produce measurable increases or at least maintain acceptable levels of abundance. Scientific monitoring and research therefore play an important role in documenting and sometimes improving MPA effectiveness.

Population connectivity can play an important role in MPA efficacy and thus represents an important consideration in design and future management. Given that not all MPAs have immediate positive effects (Agardy et al. 2011), monitoring and research to facilitate informed adaptive management decisions can improve MPA effectiveness. Scientific research and long-term monitoring programs become increasingly important in instances where MPAs fail to achieve their intended objective, or regulations result in unexpected or unwanted changes.

Traditionally, fisheries managers use a variety of harvest control rules such as licenses, quotas, fishing seasons, fishing methods, among others; still, many fish stocks continue to

decline, even when these measures are implemented (Worm et al. 2009). Collapse of northern cod (an area that encompasses the north coast of Newfoundland and the Labrador coast, defined by NAFO divisions 2J3KL), and other groundfish stocks in eastern Canada resulted in the implementation of fishing moratoria in 1992 with associated economic and social changes (Hutchings and Myers 1995). This closure now appears as a textbook reminder of the costs associated with poor fisheries management. Since the collapse of northern cod more than 20 years ago there has been no evidence of recovery above pre-moratorium abundances (DFO 2012). A small-scale directed northern cod fishery persisted in the inshore in most years since 1998 (1998-2002, 2006-present) with reported landings in the range 3,000 t to 8,000 t. Recreational fisheries were also permitted in most years.

Declines in fishery resources globally led to alternative management measures to improve conservation, including a more holistic, ecosystem-based approach to fishery management (Worm et al. 2009) and more stringent applications of traditional fisheries management measures (Hilborn et al. 2004). Multiple authors have suggested that recognizing and managing the small-scale population structure that characterizes many marine species would greatly improve fisheries management (Stephenson 1999; Rouget et al. 2003; Sterner 2007), by preserving the intraspecific biocomplexity (population structure) needed to maintain healthy ecosystems (Hilborn et al. 2003; Worm et al. 2006; Schindler et al. 2010).

Since the collapse of northern cod, several studies have recognized different inshore populations in this region based on contrasting distributions, life history characteristics and genetic differences (Lilly et al. 1999; Ruzzante et al. 2000; Beacham et al. 2002; Morris and Green 2002; Smedbol and Wroblewski 2002; Bradbury et al. 2011). Persistence of these populations at a time when offshore population abundances have remained low further attests to their importance. The Gilbert Bay MPA (Figure 2.1), which is located within NAFO division 2J, has as its primary objective the protection of the genetically unique population of Atlantic cod and its habitat (Canada Gazette 2005). This population was considered susceptible to overfishing soon after the northern cod fishery reopened in 1998, following six years of moratoria, when low abundances in other populations led fishers to target considerable and focused efforts on this small, local population (Morris and Green 2002; Morris et al. 2003). Other work describes the population as resident (Green and Wroblewski 2000), with a very localized and restricted primary overwintering and spawning site within Gilbert Bay (Chapter 3), and limited movement of individuals (Chapter 4).

These biological characteristics of the Gilbert Bay cod population (Green and Wroblewski 2000; Beacham et al 2001; Morris and Green 2002) clearly emphasized the need to protect this unique population and were important in the establishment of the Gilbert Bay Marine Protected Area. Subsequent research has identified a decline in abundance and has focused on factors affecting MPA effectiveness. This chapter presents long-term population monitoring and data analysis, including trends in abundance, size

distribution, and recruitment. The chapter also considers commercial fishing effort near the Gilbert Bay MPA from 1998 to 2011.

## 2.3 METHODS

### 2.3.1 Annual Sampling

Annual sampling methods used to study population dynamics were initially developed and described by Morris and Green (2002). Continued sampling efforts spanned 26 research and monitoring trips to Gilbert Bay from 1998-2011 (Table 2.1), during which Gilbert Bay cod were sampled in late May-early June (spring), and again in early August (summer) from small boats 4-7 m in length. Spring monitoring targeted the Gilbert Bay cod spawning season (see Chapter 3), at which time most Gilbert Bay cod were concentrated at overwintering locations (Morris and Green 2002; Morris et al. 2003). Summer monitoring targeted a period after fish (particularly adults) disperse from their overwintering areas (see Chapter 4).

### 2.3.2 Research catch data

Hook and line sampling, using a straight one ounce jigging lure (Gibbs Minnow Jig™), was conducted in order to capture representatives of nearly all size classes of Gilbert Bay cod (fish greater than ~15 cm, and ages 2- 18 yrs) from 33 sampling locations in zone 1a during each trip (Figure 2.2). Thirty other locations distributed throughout Gilbert Bay were sampled less regularly. Although this strategy samples non-randomly, it provides

relative trends in specific size classes at defined locations which does not require random sampling. The largest fish caught were comparable to commercial sizes, and commercial efforts presumably include some of the largest fish available. Sampling sites covered an average area of 2 hectares and were typically spaced 500 to 7500 meters apart within zone 1a (Figure 2.2). Most fishing locations were initially selected based on fish availability, and spanned a depth range of 5-15 m. Because sampling was non-random, total fish abundance cannot be estimated, however, the objective of this sampling was to look at relative rather than absolute change in numbers. Since 2004, the fishing times, duration, and number of people fishing at each location was recorded; data for previous years documented daily fishing effort (time and people). Each site was sampled for a minimum of 30 minutes and less than 120 minutes consecutively, and ensuring that sites were not fished sequentially.

Upon capture, each cod was measured for total length (TL) to the nearest millimeter and further examined by gently squeezing the abdomen to check for sexual maturity (identified by the presence of eggs or milt) and generally assessing overall fish condition. Healthy fish larger than 30 cm were marked with an external, individually numbered tag (Floy® t-bar tag) and released (n = 8213) at the location of capture. Some cod (n = 105) were recaptured during commercial fishing and the tags were returned to Fisheries and Oceans Canada.

Annual research catch rates were calculated for the entire time series, 1998-2011 based on mean daily catch rates 1998-2005. For 2005-2011 the calculation was based on mean

catch rate per site. Research catch per unit effort (CPUE) was defined as the number of fish caught divided by the number of people fishing multiplied by the time (hrs) each person fished, standardizing catch to the average sampling effort during the 14-year time series (i.e. annual mean effort of 178 hours of fishing each spring).

### 2.3.3 Recruitment

The relative abundance of a cohort sampled during three and four consecutive years of sampling was used to estimate the strength of each cohort relative to others in the series. These data included as many year classes as possible identified from modes in length-frequency distribution plots that were standardized by sampling effort. Modes in length-frequencies from ages 2 to 5 were distinguishable by visual inspection of data and assigned to year classes based on length-at-age data from otolilths. Ages from 2-5 years were selected because sampling collected few age 1 fish and there was considerable overlap in length at age after age 5. To convert individual lengths representing modal length groups to age, the length-frequency distribution was divided into age classes (2-5 yrs) estimated from the midpoint between mean lengths-at-age determined from otolith aging. These midpoints corresponded to modes in the length-frequency distribution. A plot of the standardized proportions by age across years (SPAY) was used to show cohort consistency (see Healey 2011 for methods). Annual proportions at age were computed and then standardized to have a mean of 0 and variance of 1. Values were calculated by subtracting the mean proportion and dividing by the standard deviation of the proportions computed across years. The same methods are used to track year classes for northern cod

(Brattey et al. 2010), American Plaice (*Hippoglossoides platessoides*) (Dwyer et al. 2012), and Greenland Halibut (*Reinhardtius hippoglossoides*) (Healey 2011).

### 2.3.4 Growth

Because a very limited number of fish were sampled for conservation reasons, otoliths were not sampled from all ages annually. Therefore, otoliths sampled in different years were combined to produce a general length-at-age relationship. To estimate the trend in growth, a Von Bertalanffy growth formula

$$L_t = L_\infty (1 - e^{-K(t_1 - t_0)})$$

was fitted to the data, where $L_\infty$ denotes the average length of a very old fish in the population, K represents a growth coefficient, $t_0$ denotes the age the fish would have at length zero, and Lt denotes the length at age t. Length and age data were obtained from fish at the same time each year during the early spring spawning period. A Ford-Walford plot (Pauly 1984) was used to estimate the Von Bertalanffy model parameters K and $L_\infty$ by rewriting the Von Bertalanffy growth formula in the form

$$L_{t+1} = a + bL_t$$

where $L_\infty = a / (1 - b)$ Eq. A

and $K = -\ln(b)$. Eq. B

The data provided an estimate of a = 9.5924 and b = 0.8565, and from equations A and B enabled the calculation of $L_\infty$ = 66.9 and K=0.1549.

### 2.3.5 Maturity

During the spawning period samples were collected to describe the age and lengths at maturity. Between 1998 and 2011 389 Gilbert Bay cod were euthanized (by direct blow to the head) prior to dissection. Fish were sacrificed if recaptured with a tag or if injured during capture with low chance of survival. All fish were measured and sexed when possible prior to removing otoliths for aging by experienced readers at the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland and Labrador. Atlantic cod ovaries and testes were staged following the method of Morrison (1991). Female fish with large ovaries and visible eggs were identified as mature, and those with small translucent ovaries as immature. Some fish with non-translucent, small ovaries were likely skip spawners, which were noted but excluded from histological analysis. Although less is known about skip spawning in male compared to female fish, available data suggests skipped spawning is less common among males (Rideout and Tomkiewicz 2011). Previous work documented skip spawning in the Gilbert Bay population based on histological analysis (Morris and Green 2002). Males were identified as mature by the presence of milt and immature when testes were small and tightly coiled. Because small testes were sometimes difficult to identify in the field, compared to small ovaries, the sex of all fish was not recorded. Unidentified individuals were likely immature males.

Logistic regression was used to fit sigmoid curves to the proportion mature by length and

age in the form,

$$p_{x_1} = \frac{e^{(b_0+b_1x_1)}}{(1+e^{(b_0+b_1x_1)})}$$ where,

$P_{x1}$ describes the probability that a fish is mature in a given length (cm) or age interval x1, and $b_0$ and $b_1$ denote parameters that define the shape and location of the fitted sigmoid curve.

The predicted length or age at 50% maturity was calculated as,

L (or A) 50 = $-b_0/b_1$.

To assess the effect of skip spawners, all fish 40 cm or larger and age 7 or older were assumed to have reached sexual maturity at least once prior to capture, and regression curves for comparison were fitted under that assumption.

### 2.3.7 Commercial fishing

Fisheries and Oceans Canada provided commercial fishing information (landings data, fishing season, number of harvesters) from dockside monitoring. For this study, landings information was selected from an area consistent with the home range of the Gilbert Bay cod population (see Chapter 4), where fishing catches were likely to include Gilbert Bay cod. Commercial catch was compared with sampling data using Pearson correlation.

Recaptures of externally tagged cod by commercial and recreational harvesters during the commercial and recreational fishing season provided an indication of size of fish caught, fishing locations, and the timing of recapture in areas outside the MPA.

## 2.4 RESULTS

Research sampling catch rates were highest in 1998, 6 years after the northern cod fishing moratorium commenced, and have declined thereafter (Figure 2.3). Catch rates typically varied among sites and years. A two-way ANOVA comparing 10 consistently fished and well-distributed sites within zone 1a from 2005-2011 found no significant within-year differences among sites (P=0.074), however a significant year effect was evident (P=0.010) (Table 2.2). Catch rate decreased significantly between 2005 and 2010 (Tukey's pairwise multiple comparison P=0.023). Although the ANOVA analysis failed a test of normality, it passed a test of equal variance (Sigma-Stat 3.0); ANOVA is relatively robust to normality issues and the result was consistent with general trends through the sampling period (1998-2011).

The biomass of Gilbert Bay cod sampled decreased during the 14-year sampling period, and remained particularly low after 2008. The proportion of the biomass sampled since 2008 was between four and 11 times lower than in 1998 (Figure 2.3). From 1998-2006, at least 1 fish per 30 minute fishing interval was caught when sampling at different sites within zone 1a. During each year since then, however, at least one 30-minute sampling

period occurred when not one fish was caught at some regularly sampled sites. Moreover, during 14 years of research sampling and more than 26 sampling trips, we captured and released 11,738 fish in zone 1a; of which only 28 individuals were a species other than Atlantic cod. Given that sampling from a variety of locations elsewhere demonstrates that this method collects a wide range of species effectively (personal observation), the results strongly suggest that cod were, by far, the predominant fish species in Gilbert Bay. Indeed, 2009 marked the first time that a fish other than Atlantic cod was caught in zone 1a. Since then several different species including rock cod (*Gadus ogac*), sculpin (*Myoxocephalus scorpius*), and flounder (*Pseudopleuronectes americanus*) have been captured in zone 1a during both spring and summer sampling. In contrast, these species were not uncommon in samples from zone 3 and other coastal areas.

Length data collected since 1998 describe striking recruitment trends in the Gilbert Bay cod population. Modes representing a specific year class were sampled consistently in different years of sampling, providing estimates of year class strength over consecutive years. Standardized length frequency distributions (Figures 2.4 and 2.5) helped depict the relative abundance of year classes. For example, cod between 13.7-21.3 cm TL (age 2) in 2003, 21.4-27.8 (age 3) in 2004, 27.9-33.4 (age 4) in 2005, and 33.5-38.2 (age 5) in 2006 were abundant compared to fish of the same size in the subsequent year. Other year classes showed a similar pattern. A recruitment pattern characterized by years of strong recruitment followed years of weak recruitment (Figure 2.6).

The length-at-age relationship for Gilbert Bay cod provides an indication of the time (years) required for year classes to reach commercial size (Figure 2.7). The data suggest that the series of relatively strong year classes produced from 1999 to 2002 would have reached a minimum commercial size (45 cm) at age 7, during 2006 to 2009. The timing of recruitment to the fishery of these 4 strong year classes overlapped a period of relatively high commercial landings within recent years (Table 2.3). However, landings decreased during that time period, from 17,500 to 9500 kg. Assuming that the commercial fishery exploited these strong year classes, as suggested by their disappearance from length-frequency distributions (Figure 2.4), the strong relationship between CPUE and commercial fishing (Figure 2.8), and the relatively weak year classes from 2003-2005 (Figure 2.6), the poor research catches in recent years (2010-2011) are hardly surprising. Indeed few fish were caught at ages 6 -13 years (35-55) and low abundances of fish > 45 cm were sampled in recent years (2008-2011) (Figure 2.8). A relatively strong 2006 year class should produce the next significant year class to reach commercial size in 2013. The length-frequency distribution from 2011 indicates that the 2009 year class (and possibly the 2008 year class) could also be strong, based on relatively high numbers of age 2 and 3 year olds sampled in 2011 (Figure 2.4 and 2.5).

### 2.5 1 Commercial recaptures

One hundred and five tags were returned from commercial fishing activities since 1998. Of those recaptures, 49 were caught outside the MPA after 2000. Fifty six tagged fish were caught within Gilbert Bay in 1998 and 1999, before the MPA was established. Fish

caught during commercial fishing were usually larger than 45 cm (Figure 2.9). The furthest distances tagged Gilbert Bay cod were reported captured were Alexis Bay and areas along the coast, corresponding to distances of approximately 10 km north and 20 km south of the MPA boundary. One tagged cod was reported captured 60 km south of Gilbert Bay in 2001.

### 2.5.2 Maturity

Between 1998 and 2011 the length, age, and sexual maturity status of 100 female, 197 male, and 92 immature fish for which sex were not determined were collected (Table 2.4). It was assumed that small immature fish not identified in the field were male. In logistic curves describing length and age at which males and females reached maturity (Figure 2.10), male Atlantic cod were estimated to be 50% mature at a length of 30.5-34.4 cm (Table 2.4), and at an age of 3.9-5.1 yrs. Assuming that immature fish were male increased the length at maturity by 3.9 cm and 1.2 years. Females matured over a greater range in size, but skip spawners likely biased these observations. Fifteen large female fish were likely skip spawners, based on observations of their ovaries. With potential skip spawners included, female Atlantic cod were 50% mature at 34.9 - 38.2 cm (Figure 2.3) and at 5 - 5.8 years. When data were analyzed excluding the expected skip spawners, females matured over a similar range as the males.

## 2.6 DISCUSSION

The objective of the Gilbert Bay MPA is to protect the genetically distinctive Atlantic cod population and its habitat (Canada Gazette 2005), and there is clear evidence that the MPA protects the population's most important spawning area and also protects many Gilbert Bay cod until sexual maturity (Chapter 4?). However, because Gilbert Bay cod are migratory (Chapter 4) some are harvested after they attain commercial size (7 years old and 45 cm TL) and move outside the MPA. This study documented a significant decline in the protected Gilbert Bay Atlantic cod population and its likely causes. From a fishery enhancement perspective (which is not the MPA's explicit mandate) the decline in the abundance of sexually mature, commercial size fish demonstrates limitations in the MPA.

From the 1970's until 1992, commercial fishing was conducted in Gilbert Bay (Powell 1987; Morris et al. 2001b) and presumably reduced the abundance of Gilbert Bay cod. The 1998 length frequency distribution shows an abundance of fish between 35 and 50 cm (ages 4-9) and few larger fish, suggesting a low abundance of commercial sized fish in 1992 and some population rebuilding between 1992 and 1998. Commercial fishing directly within Gilbert Bay resumed in 1998 and 1999, which correlated with the observed decline in research catch rates. Reported landings in 1998 and 1999 of 18,000 and 16,000 kg respectively from the Gilbert Bay population (as reported by Morris et al. 2003) significantly impacted the total population, which was likely less than 100,000 kg

at that time (Morris et al. 2003). Continued fishing within Gilbert Bay at this intensity during a period of poor recruitment would have greatly reduced population size over a short time period.

In those instances where a relatively strong year class was detected, even at age 2 (13.7-21.3 cm TL), it was possible to follow a cohort until at least age 4 or 5, when modal analysis was no longer possible. More detailed information on year class strengths beyond age 5 requires increased lethal sampling to remove otoliths from many individuals. Lethal sampling was minimized in the Gilbert Bay monitoring program for obvious conservation reasons, and no attempt was made to resolve year class abundance or differences in growth for all cohorts on an annual basis. Therefore, trends in the abundance of cod were inferred based on interpretation of length-frequency distributions and catch per unit effort data. Catches of demersal juvenile cod (ages 2 and 3 yrs) and those that potentially reached sexual maturity (4-5 yrs) provide consistent information concerning recruitment-driven demographic changes in the Gilbert Bay cod population.

Several ultrasonic tagging and tracking studies conducted since 1998 investigated the movement patterns of cod in Gilbert Bay, and raised the questions of whether all Gilbert Bay cod home (and by what mechanisms) and over what spatial and temporal scale (Chapter 4). Collectively during these studies size-specific behavior, seasonal migration patterns and foraging movements within and in areas adjacent to Gilbert Bay have been described (Green and Wroblewski 2000; Morris and Green 2002; Chapter 4; Chapter 5). These investigations show that Gilbert Bay cod are site specific and return to the same

areas of zone 1a each year. Importantly, they also showed that some Gilbert bay cod move outside the MPA where commercial harvesting occurs.

A reduced number of mature spawners and several years of poor recruitment truncated the natural age and size distribution, leaving fewer strong year classes. Reestablishing greater numbers of larger and mature Gilbert Bay cod could provide improved and more sustainable local harvesting benefits on a small scale. Monitoring indicates recent strong year classes not yet recruited to commercial size, and, with the acquired knowledge of fishery effects on the population, future work to develop a quantitative population model using existing and new monitoring data could provide a useful adaptive management tool.

The level of commercial Atlantic cod fishing effort and landings increased in the vicinity of Gilbert Bay in recent years, particularly since 2007. Maddock-Parsons and Stead (2009) report increased sentinel fishery catch rates in the vicinity of Gilbert Bay during 2007-2008. Catch rates increased from 1-3 fish per net to 5-6 fish per net, a modest increase but perhaps reflective of the potential output from a small local population such as the Gilbert Bay cod population. The increased catch corresponds to the timing of relatively strong year classes produced during the 1999-2002 period which would have reached commercial size during the period of increased landings from sentinel fishing. Tagged Gilbert Bay cod were caught at each of these locations in the past, demonstrating that some Gilbert Bay cod move to these areas. However, tag returns from commercial fishing are not easily comparable to research tag-recapture rates. Reporting rates of commercial tag recaptures are considered inaccurate in terms of location and fish size,

and periodic disputes between harvesters and MPA management result in low and variable reporting rates over time. The potential export of fish from Gilbert Bay, however, is not spillover, which would constitute a net export of fish from an MPA. The data suggests very limited spillover from Gilbert Bay, because the large migratory Gilbert Bay cod that move outside the MPA in summer return to Gilbert Bay each fall.

Declining research catch rates, the removal of large fish during commercial fishing, and periods of poor recruitment indicate substantial changes to the Gilbert Bay cod population. The recent absence of cod at some sampling sites on the spawning grounds recently and the occurrence of fish species other than cod in recent years could be related. If this trend continues, long-term changes in local fish community structure may follow. Given reports of local Atlantic cod population disappearances in Maine (Ames 2007), it is possible that population dynamics at very low levels of abundance are currently difficult to predict,, potentially driven by equally unpredictable factors such as weak or nonexistent compensation, allee effects or density independent effects as stock size declines (Keith and Hutchings 2012).

## 2.7 CONCLUSIONS

This research and monitoring demonstrated substantial changes in Gilbert Bay cod population demographics. Protecting discrete populations that could be engulfed by large scale fishery management areas, such as the northern cod management area (NAFO 2J3KL), requires some understanding of population connectivity. Fishing in Gilbert Bay

during 1998 and 1999 prior to MPA regulations and the increased fishing activity in areas surrounding the MPA during the period from 2007 to 2011, has led to a substantial decrease in the Gilbert Bay cod population. Although the MPA protects important spawning and nursery habitats, as well as some young adults and foraging/feeding habitats, its effectiveness can be improved. In this case, the goal of the MPA is to protect the Gilbert Bay cod population and its habitat, but whether this MPA can contribute to the recovery of cod in other areas remains unknown. Despite variable recruitment, our work provides evidence of relatively strong recruitment in 2006 and possibly 2009 but these fish have not yet reached commercial size. Strong recruitment did occur in some years with low population levels but the variability in recruitment suggests that protecting these year classes and maintaining a larger adult population will help the probability of rebuilding the Gilbert Bay cod population if adaptive management measures are implemented. Early life history and recruitment information represents an important component of understanding population connectivity, which is considered in the next chapter.

Table 2.1. Summary of angling research data collected in zone 1a, within Gilbert Bay during spring and summer sampling periods, from 1998 to 2011.

| Year | Sampling period | Rod hrs | Fish caught |
|---|---|---|---|
| 1998 | June 1-10 | 88 | 439 |
| 1999 | May 20 -June 2 | 168 | 598 |
| 2000 | June 10-22 | 148 | 447 |
| 2001 | May 29 - June 7 | 84 | 306 |
| 2002 | June 11 - 19 | 162 | 679 |
| 2003 | June 4 - 10 | 128 | 333 |
| 2004 | June 1-8 | 126 | 498 |
| 2005 | June 1-19 | 222 | 675 |
| 2006 | June 1-10 | 224 | 602 |
| 2007 | June 1-10 | 224 | 457 |
| 2008 | June 2-12 | 284 | 418 |
| 2009 | June 2-11 | 274 | 491 |
| 2010 | June3-10 | 231 | 366 |
| 2011 | June 1-9 | 165 | 408 |
| | | | |
| 1998 | July 27-August 3 | 23 | 183 |
| 1999 | August 2-12 | 30 | 314 |
| 2000 | | | |
| 2001 | July 30 - August 5 | 39 | 210 |
| 2002 | July 31 - August 6 | 51 | 424 |
| 2003 | | | |
| 2004 | August 1-7 | 54 | 298 |
| 2005 | August 2- 8 | 63 | 329 |
| 2006 | July 31 - August 5 | 50 | 475 |
| 2007 | July 31- August 7 | 73 | 290 |
| 2008 | August 2-11 | 206 | 372 |
| 2009 | August 2-10 | 191 | 538 |
| 2010 | August 3-8 | 101 | 610 |
| 2011 | August 1-5 | 191 | 415 |

Table 2.2. Two-Way ANOVA comparing CPUE among 10 common fishing sites and seven sampling years (2005-2011).

| Source of Variation | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Site | 10 | 28.573 | 2.857 | 1.833 | 0.074 |
| Year | 6 | 29.958 | 4.826 | 3.097 | 0.010 |
| Residual | 60 | 93.511 | 1.559 | | |
| Total | 76 | 151.042 | 1.987 | | |

Table 2.3. Commercial Atlantic cod catches (round weight) reported by Department of Fisheries and Oceans dockside monitoring program at locations where tagged Gilbert Bay cod were caught and reported by commercial fishermen. Fishing areas span headland areas between Salmon Point (N 52° 37' 44", W 55° 44' 51") in the north, to Cape Spear (N 52° 26' 35", W 55° 37' 38") to the south, and all of Alexis Bay. The northern cod fishery was closed from 2003-2005.

| Year | Active Fishermen | Total catch (kg) | Individual Quota (kg) | % quota caught |
|---|---|---|---|---|
| 1998 | 12 | 8,135 | 1125 | 60 |
| 1999 | 11 | 12,057 | 4082 | 27 |
| 2000 | 3 | 613 | 3810 | 5 |
| 2001 | 2 | 928 | 3810 | 12 |
| 2002 | 9 | 5,740 | 3810 | 17 |
| 2003 | | | | |
| 2004 | | No Fishery | | |
| 2005 | | | | |
| 2006 | 10 | 6,598 | 1361 | 48 |
| 2007 | 19 | 17,672 | 1134 | 82 |
| 2008 | 23 | 17,631 | 1474 | 67 |
| 2009 | 17 | 14,385 | 1700 | 50 |
| 2010 | 14 | 11,500 | 1700 | 48 |
| 2011 | 11 | 9,400 | 1700 | 50 |

Table 2.4. Results of logistic regression analysis of maturity status of Gilbert Bay cod versus length (cm) and age (y), with lengths ($L_{50}$) and age ($L_{50}$) at 50% maturity indicated.

| Group | Sample size | Independent variable | $L_{50}$ or $A_{50}$ | | Coefficients | Standard error | p-value |
|---|---|---|---|---|---|---|---|
| Males (excluding immatures) | 197 | Length | 30.5 | Constant | -10.129 | 3.048 | <0.001 |
| | | | | Length | 0.332 | 0.086 | <0.001 |
| | | Age | 3.9 | Constant | -4.569 | 1.583 | 0.004 |
| | | | | Age | 1.167 | 0.288 | <0.001 |
| Males (including immatures) | 289 | Length | 34.4 | Constant | -17.299 | 3.012 | <0.001 |
| | | | | Length | 0.503 | 0.087 | <0.001 |
| | | Age | 5.1 | Constant | -8.167 | 1.129 | <0.001 |
| | | | | Age | 1.610 | 0.219 | <0.001 |
| Females (including skip spawners) | 100 | Length | 38.2 | Constant | -6.192 | 1.479 | <0.001 |
| | | | | Length | 0.162 | 0.038 | <0.001 |
| | | Age | 5.8 | Constant | -3.238 | 0.903 | <0.001 |
| | | | | Age | 0.555 | 0.143 | <0.001 |
| Females (assuming mat at 40 cm and 7 yr) | 100 | Length | 34.9 | Constant | -21.441 | 5.207 | <0.001 |
| | | | | Length | 0.613 | 0.148 | <0.001 |
| | | Age | 5 | Constant | -17.023 | 5.048 | <0.001 |
| | | | | Age | 3.396 | 0.997 | <0.001 |
| Males and females combined | 389 | Length | 35.4 | Constant | -9.262 | 1.016 | <0.001 |
| | | | | Length | 0.262 | 0.027 | <0.001 |
| | | Age | 5.3 | Constant | -6.225 | 0.689 | <0.001 |
| | | | | Age | 1.173 | 0.123 | <0.001 |

Figure 2.1 Map of study area showing the Gilbert Bay MPA. Colours represent different MPA zones established for different regulations (see Canada Gazette (2005) for regulatory details).

Figure 2.1

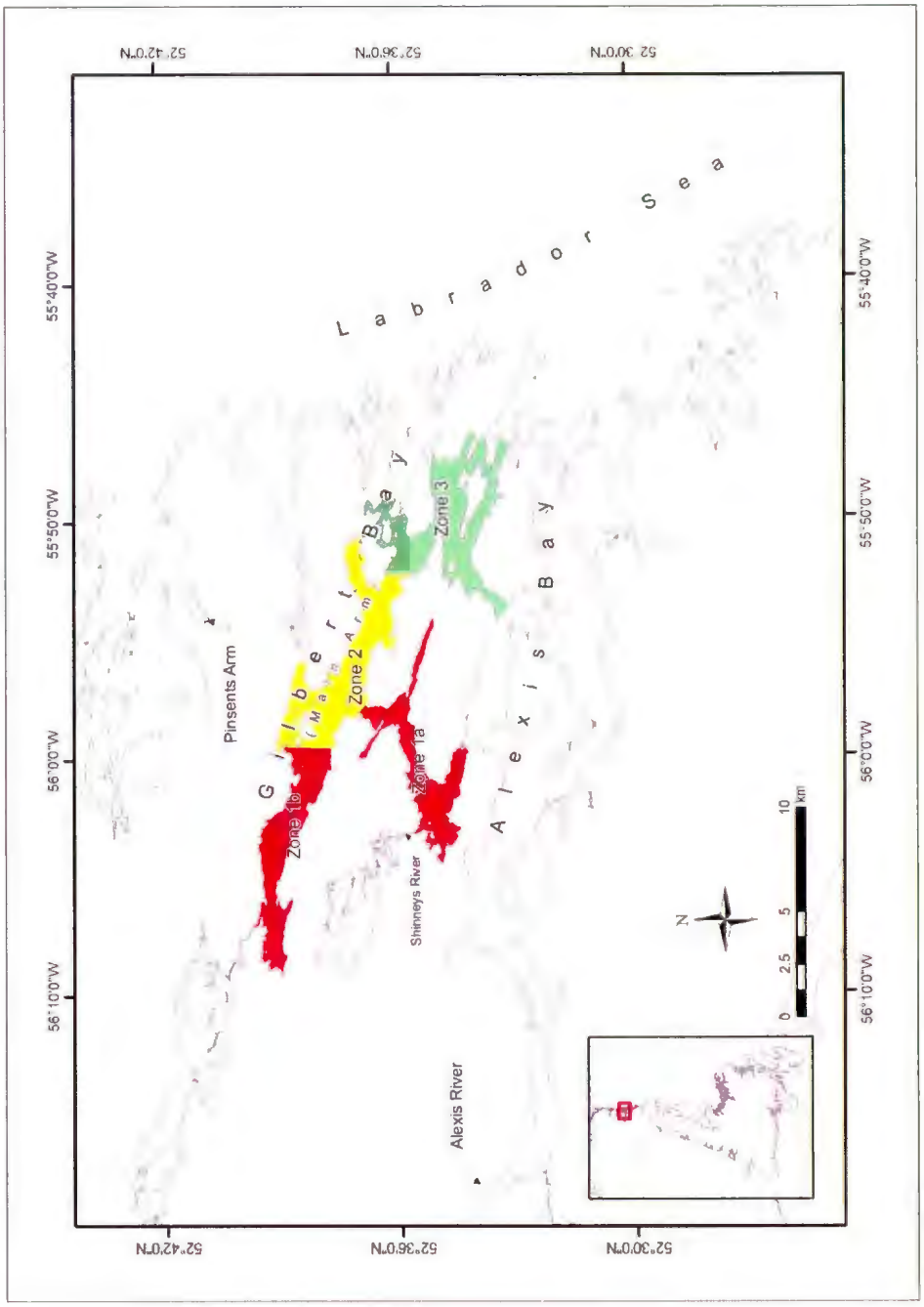

52°42'0"N
52°36'0"N
52°30'0"N
55°40'0"W
55°50'0"W
56°0'0"W
56°10'0"W
Labrador Sea
Alexis Bay
Gilbert Bay
Pinsents Arm
Zone 1b
Zone 2
Zone 1a
Zone 3
Shinneys River
Alexis River
N
0
2.5
5
10
km

Figure 2.2. Sampling locations (dark blue boxes) in zone 1a, also referred to as The Shinneys.

Figure 2.2

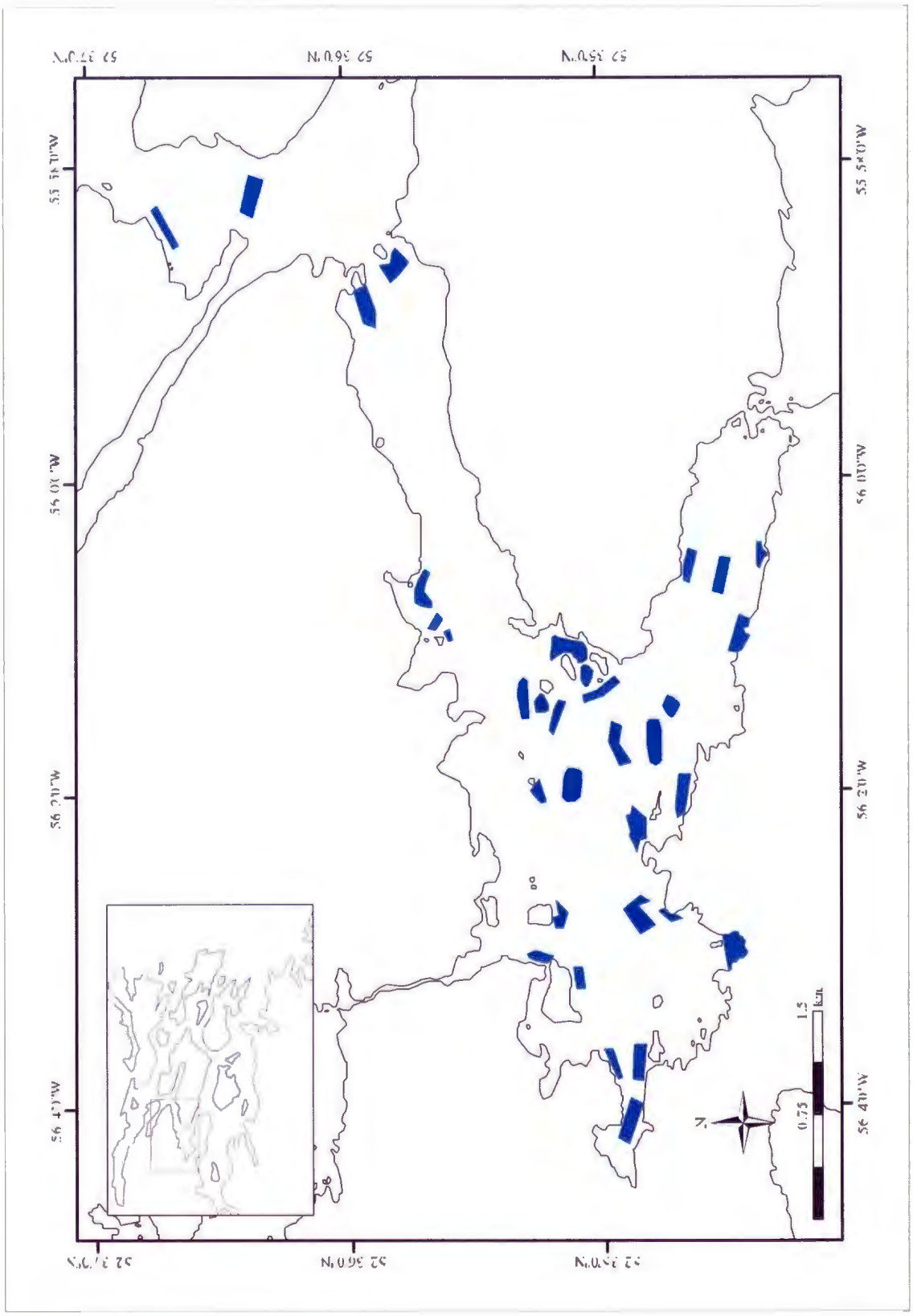


Figure 2.3. Annual research catch per unit effort (CPUE) data (mean ± SE) based on sampling in zone 1a. CPUE on the solid line describes mean daily sampling effort; CPUE on the dashed line describes individual site effort. The pink squares denote the total standardized biomass of cod sampled each year. Lower biomass in relation to CPUE, particularly since 2007, indicates fewer large fish were sampled.

Figure 2.3

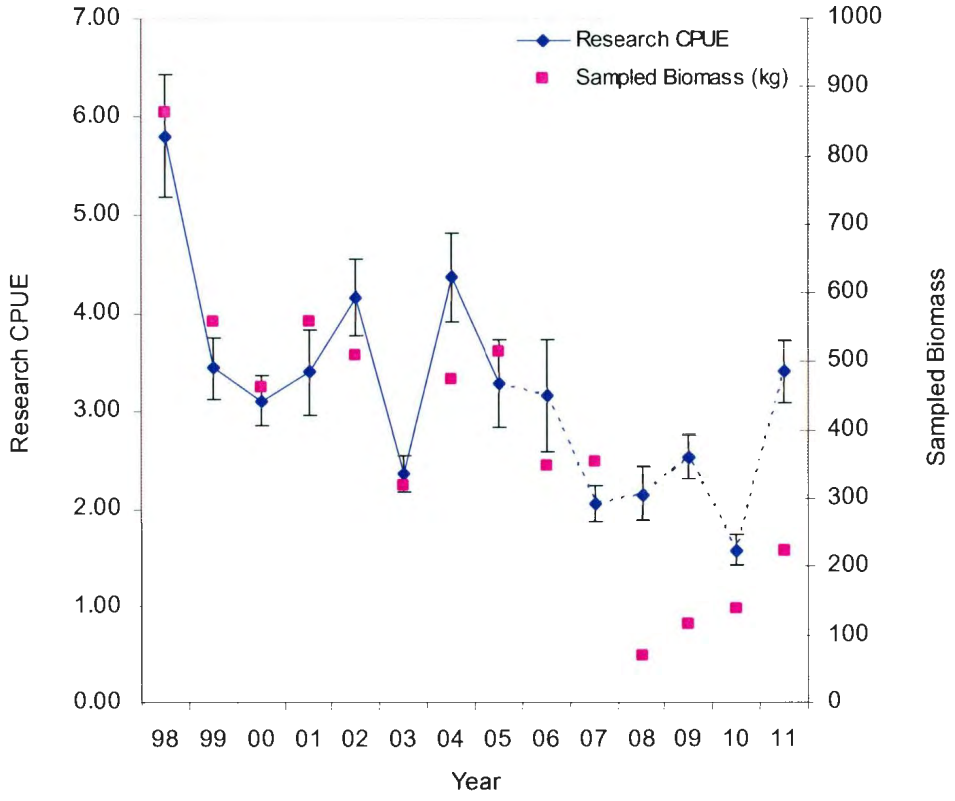

Research CPUE
Sampled Biomass (kg)
Research CPUE
Sampled Biomass
Year
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
1000
900
800
700
600
500
400
300
200
100
0
98 99 00 01 02 03 04 05 06 07 08 09 10 11

Figure 2.4 Standardized spring length-frequency distributions (see Methods 2.3.2) sampled in zone 1a. Given the desire to limit lethal sampling, particularly for large mature fish, no age frequencies were obtained.

Figure 2.4

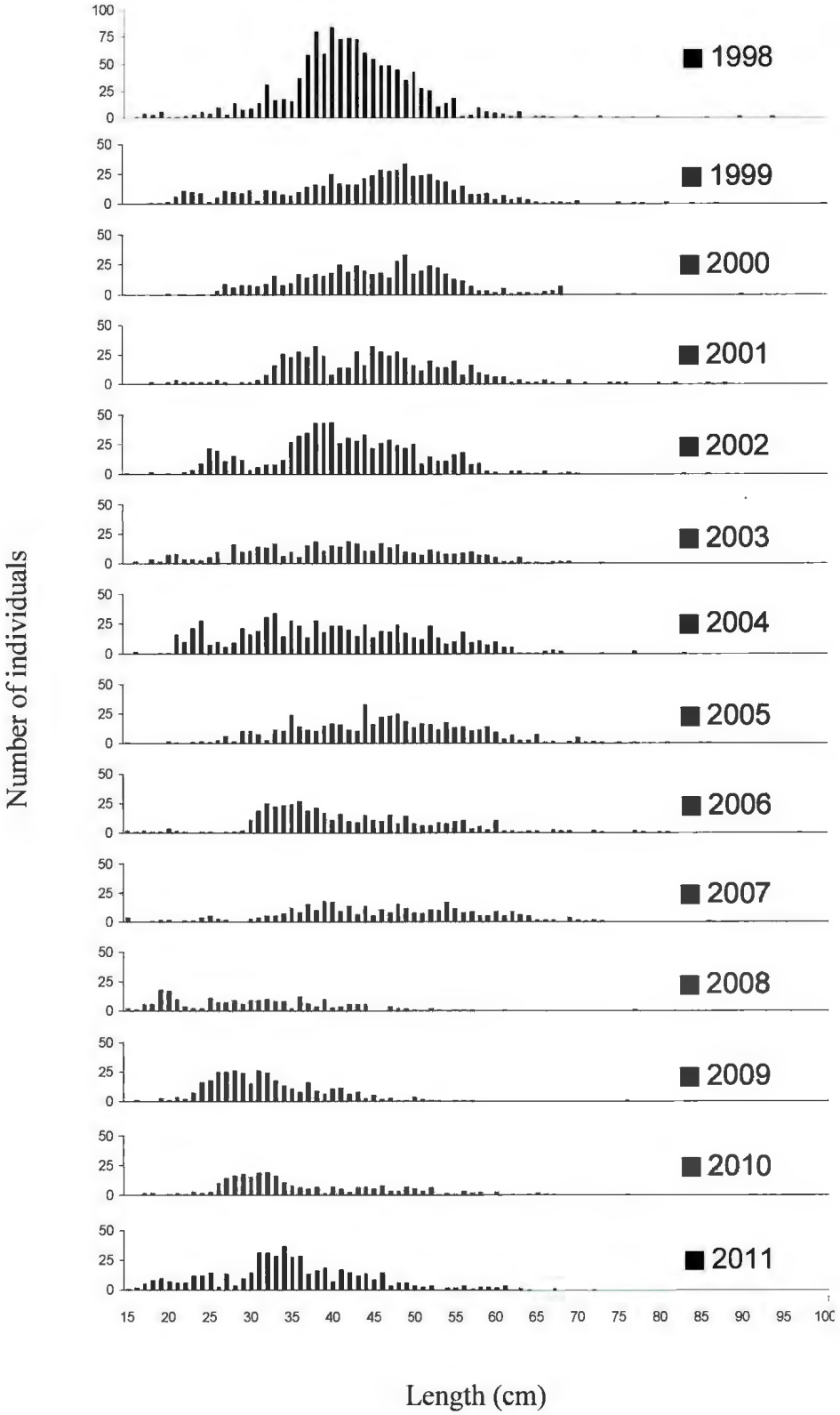

Number of individuals
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
Length (cm)

Figure 2.5. Standardized summer length-frequency distributions sampled in zone 1a.

Figure 2.5

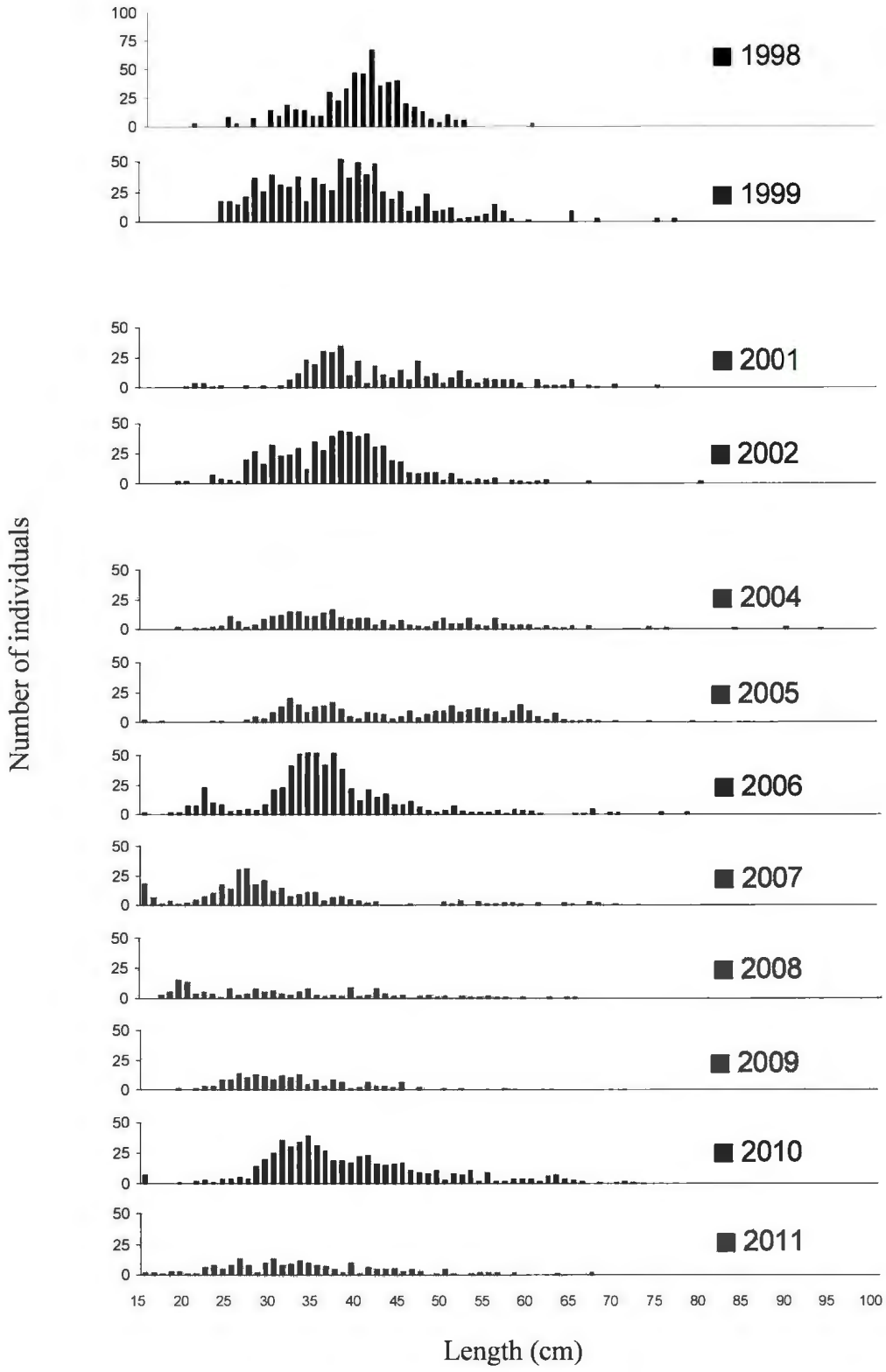

Number of individuals
1998
1999
2001
2002
2004
2005
2006
2007
2008
2009
2010
2011
15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
Length (cm)

Figure 2.6. Recruitment trends based on standardized proportions at age from spring sampling in Gilbert Bay. For each age, annual catch proportions at age are standardized to have a mean 0 and variance of 1. The size (i.e. area) of each symbol is proportional to the absolute value of the deviation. Positive deviations are shown as grey circles, and negative deviations are shown black circles. Grey and black dotted lines illustrate the consistency of both strong and weak recruitment patterns observed during four consecutive years of sampling. The symbol sizes do not reflect the year to year changes in relative strength of year classes, but are useful for indicating how consistently individual year classes track through successive surveys.

Figure 2.6

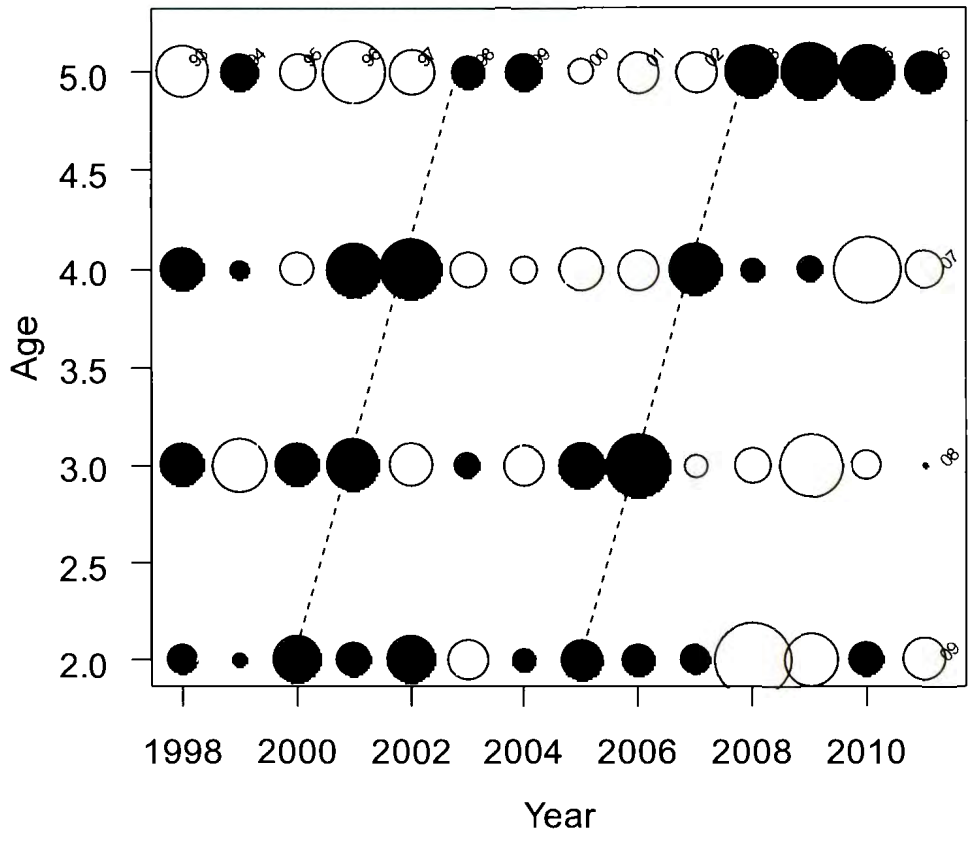


Figure 2.7. Mean length at age of cod in Gilbert Bay, where black error bars indicate standard deviation and red bars indicate range in length at age. A Von Bertalanffy growth curve was fitted to the data.

Figure 2.7

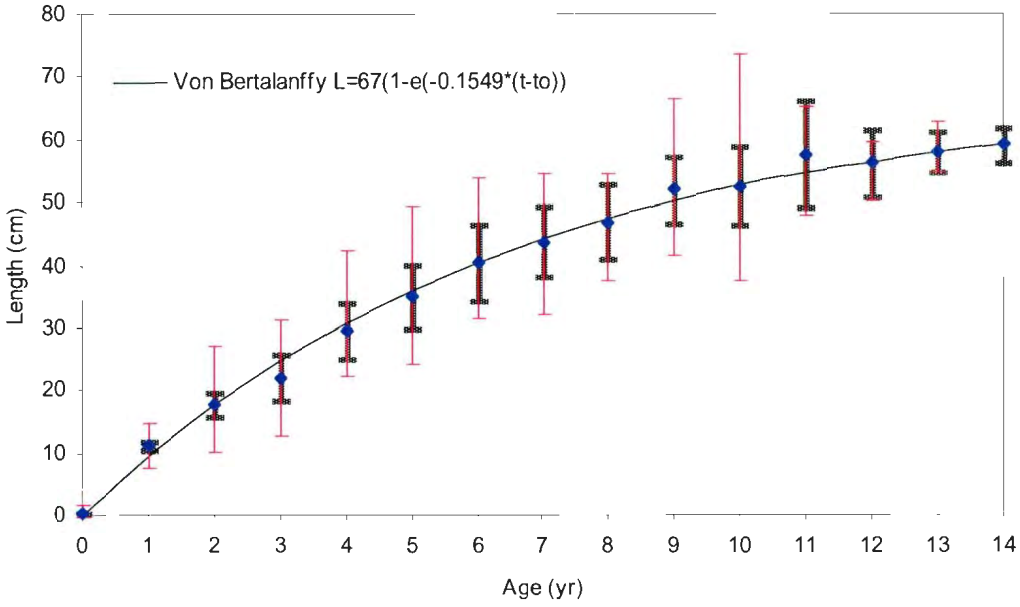

Von Bertalanffy L=67(1-e(-0.1549*(t-to))
Length (cm)
Age (yr)
0
10
20
30
40
50
60
70
80
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Figure 2.8. Number of commercial-size Gilbert Bay cod (>45 cm) sampled during research collections in Gilbert Bay (blue diamonds, primary y axis), and commercial reported landings data (Secondary y axis – hatched bars). Cod larger than 45 cm were selected because they are caught commercially (Figure 2.9). The 2006 research sampling estimate (pink circle) is known to be low and underestimates large cod because large cod migrated early during 2006 and large cod were under-sampled at the spawning site (Chapter 4). The Pearson correlation between reported landings and change in the number of commercial-sized fish sampled between years was significant, $r = -0.87$, $p = 0.002$ (with 2006 data removed as an outlier) from 1998 until 2008, after which the number of large fish has remained low.

Figure 2.8

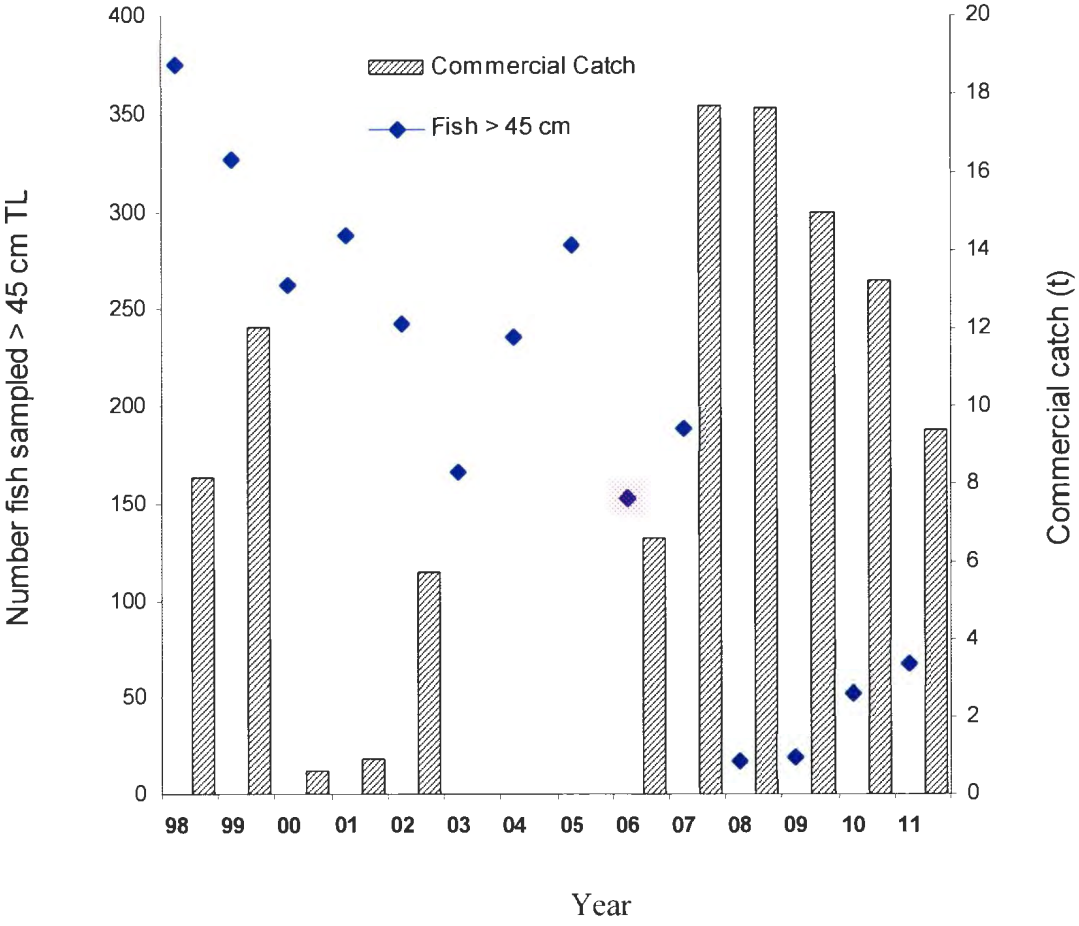
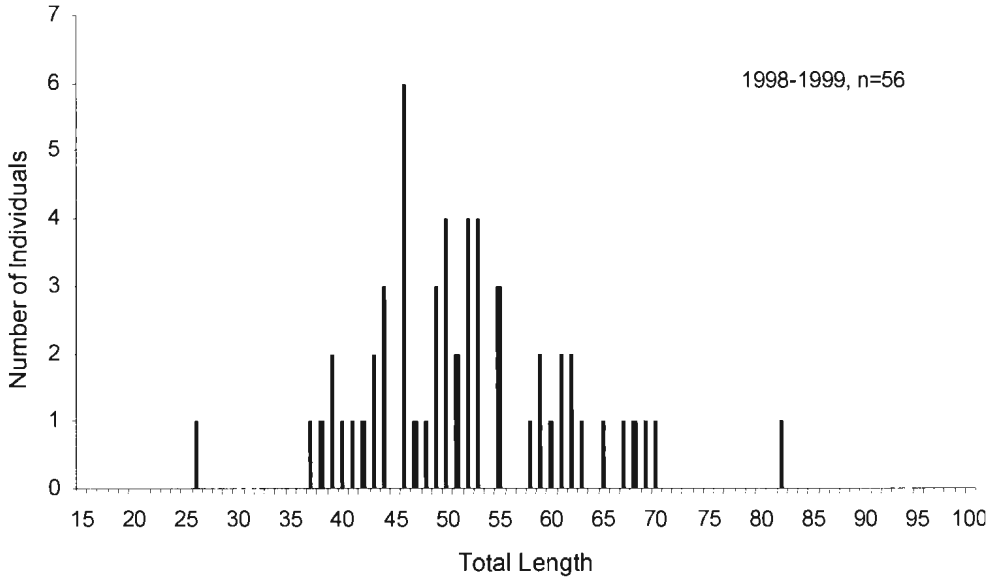

Commercial Catch
Fish > 45 cm
Number fish sampled > 45 cm TL
Commercial catch (t)
Year
400
350
300
250
200
150
100
50
0
20
18
16
14
12
10
8
6
4
2
0
98
99
00
01
02
03
04
05
06
07
08
09
10
11

Figure 2.9 Length-frequency distribution of tagged Gilbert Bay cod recaptured during commercial fishing. Top panel includes recaptures from within Gilbert Bay, zones 1b, 2, and 3 during 1998 and 1999. Bottom panel includes recaptures from outside the MPA during 2000-2008.

Figure 2.9


1998-1999, n=56
Number of Individuals
Total Length
0
1
2
3
4
5
6
7
15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100

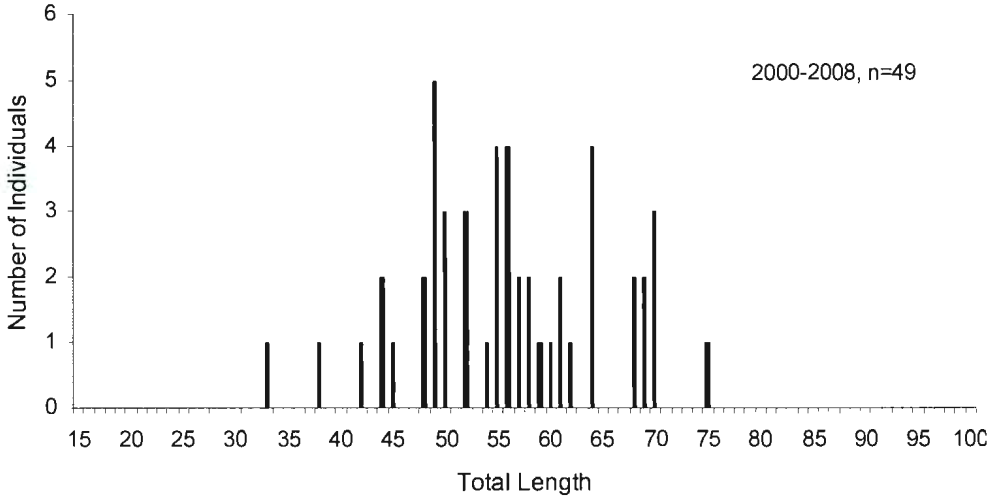
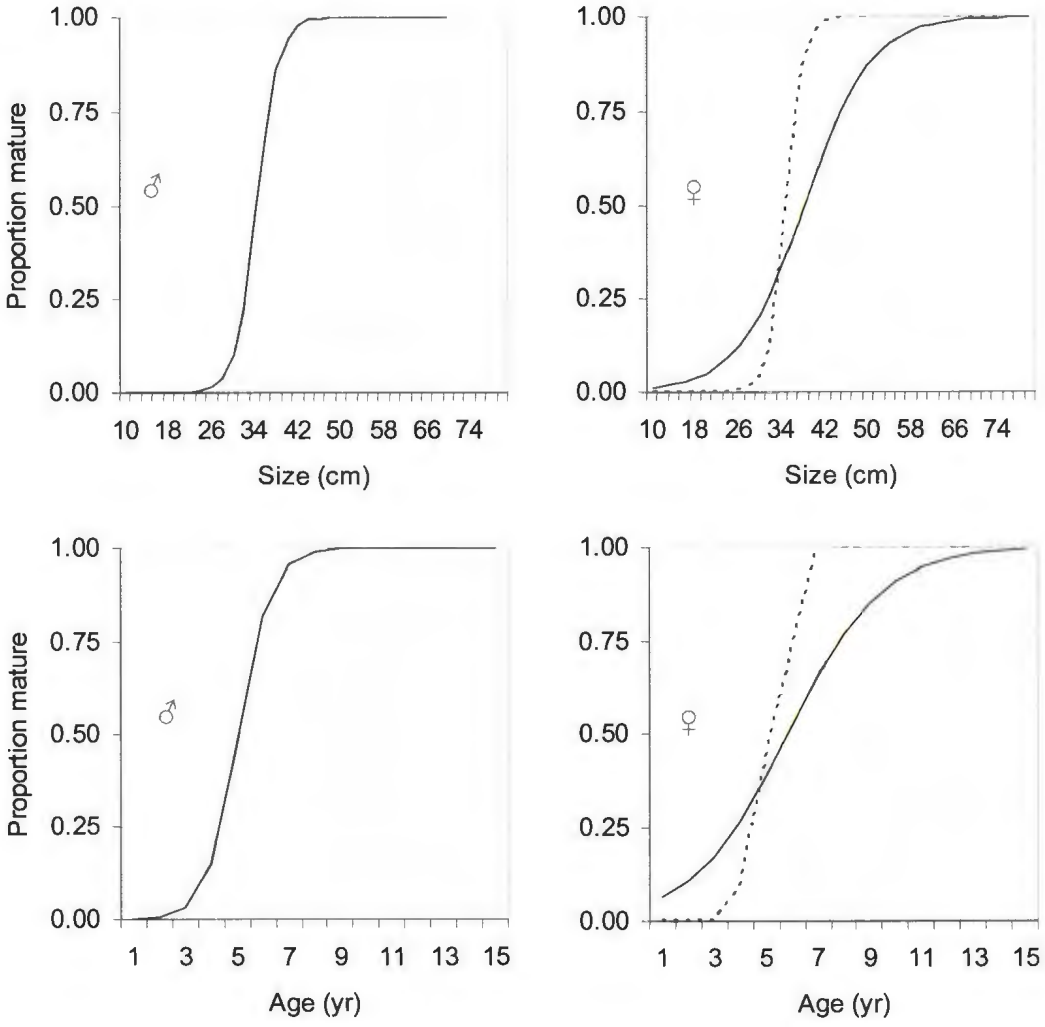

2000-2008, n=49
Number of Individuals
Total Length
0
1
2
3
4
5
6
15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100

Figure 2.10. Proportion of mature male and female Atlantic cod by length and age showing fitted logistic curves with constants from Table 2.3. Two curves are plotted for female fish, the dashed line assumes that all female fish matured by age 7 and 40 cm TL, and that those not in spawning condition were skip spawners.

Figure 2.10


1.00
0.75
0.50
0.25
0.00
Proportion mature
♂
10 18 26 34 42 50 58 66 74
Size (cm)
♀
1 3 5 7 9 11 13 15
Age (yr)

## Chapter Three

## Spawning behaviour attuned to local oceanographic features drives reproductive isolation of Atlantic cod in Gilbert Bay, Labrador

### 3.1 ABSTRACT

During 14 years of research and monitoring, resident Atlantic cod in Gilbert Bay, Labrador spawned at the same primary site near the head of the bay. Each year spawning began in May and ended in June. Eggs were confined to a layer below a 3-5 m thick surface layer of low salinity water covering the spawning site. Shallow, 5-m deep sills separate the spawning site where higher densities of eggs (23-90 egg·m$^{-3}$) were sampled, from the adjacent Main Arm where egg densities were much lower (4-7 egg·m$^{-3}$). Ichthyoplankton sampling at the same areas in early August yielded pelagic juveniles (mean length 24.9 mm) and no cod eggs. A combination of physical and oceanographic factors and locally adaptive behavioural attributes of Gilbert Bay cod maintains reproductive isolation in this genetically distinctive bay population of Atlantic cod.

### 3.2 INTRODUCTION

Traditionally, biologists have viewed marine species as having demographically open populations interconnected by high gene flow. However, multiple lines of evidence now suggest lower connectivity and greater spatial structure in marine populations than previously thought (reviewed by Palumbi 2004, Kritzer and Sale 2004; Levin 2006; Sale

et al. 2006; Gaines and Gaylor 2007). Throughout the range of Atlantic cod, geographic features such as continental shelves, continental slopes, specific coastal areas and bays, and semi-enclosed fjords help define heterotypic groups of fish (i.e. populations, sub-populations, and races) (Skjaeraasen et al. 2011; Robichaud and Rose 2004), that differ genetically (Bradbury et al. 2011; Knutsen et al. 2007) and behaviourally (Salvanes et al. 2004). Environmental heterogeneity across a species' geographic range should exert local selection pressures on the fitness of individuals within specific environments (Fraser et al. 2011), potentially resulting in locally adapted populations with important conservation value (Hilborn et al. 2003; Schindler et al. 2010). Restricted gene flow among populations increases the potential for local adaptation (Endler 1977; Slatkin 1987; Hendry and Taylor 2004; Conover et al. 2006). However, genetic differentiation may still arise among overlapping populations in cases of strong selection following dispersal (Slatkin 1987; Hedgecock et al. 2007; Marshall et al. 2010). The dispersal of eggs and larvae can therefore significantly affect population structuring, demographics, and connectivity.

Population connectivity, defined here as the exchange of individuals among subpopulations (Cowen et al. 2007), is important to understanding the potential geographic scale of local adaptation. Local adaptation refers to populations that differentiated genetically under conditions where limited dispersal or active habitat choice results in low gene flow (Kawecki and Ebert 2004). Contemporary evolutionary theory suggests that the extent to which local adaptation can occur in a species depends on population size, level of gene flow, and selection pressures acting on each individual

(Felenstein 1976, Endler 1977). Adaptive differentiation can occur rapidly (Hendry et al. 2002) over small spatial scales (Grosberg and Cunningham 2001; Hedgecock et al. 2007; Olsen et al. 2008) despite gene flow (Marshall et al. 2010), selecting phenotypic traits that directly influence the viability of populations (Conover et al. 2006). However, conclusively demonstrating adaptation in field studies remains a challenge because of limitations in linking phenotypic differences with specific genes that affect fitness. Recent reviews indicate that many species with broad geographic ranges show adaptive differentiation among populations, which can generate a variety of spatial patterns, ranging from counter gradient variation across a latitude gradient (Conover et al. 2006, 2009) to more complex geographic mosaics of adaptation (Thompson 1999). Atlantic cod populations display both of these patterns (Purchase and Brown 2000; Knutson et al. 2007; Olsen et al. 2008; Bradbury et al. 2010).

Dispersal of fish eggs, including Atlantic cod, can affect population connectivity. Dispersal depends initially on the spawning location and subsequent physical conditions to which eggs are exposed (Swearer et al. 1999; Warner and Cowen 2002; Knutsen et al. 2007; Werner et al. 2007; Ciannelli et al. 2010). Atlantic cod spawn pelagic eggs and presumably eggs spawned in offshore areas disperse more broadly (Pepin and Helbig 1997) than eggs spawned within more protected bays and fjords (Ciannelli et al. 2010).

Atlantic cod prefer to spawn at temperatures between 4 and 7 °C (ICES 2005; Righton et al. 2010), but eggs can tolerate a much larger temperature range spanning from -1.5 to 12 °C (Pepin and Helbig 1997; Jordaan and King 2003; ICES 2005; Geffen et al. 2006).

Water density, developmental stage, egg quality, and size all affect cod egg buoyancy (Sundby 1983). Depending on locality in the western Atlantic, reported densities of Atlantic cod eggs vary between 22-26 $kg \cdot m^{-3}$, with slightly positive buoyancy that facilitates eggs drifting and hatching near the surface (Anderson and de Young 1995; Ouellet 1997). At their preferred temperatures (4-7 °C) cod eggs develop quickly. Anderson and deYoung (1995) estimated that cod eggs on the northeastern Newfoundland shelf hatch in 24-27 days at 3 °C, and that stage 1 eggs (using the Markel and Frost 1985 staging scheme) are 6-7 days post-spawning at most. After eggs hatch, temperature continues to affect larval growth (Folkvord 2005 and references therein), but other factors including light (Puvanendran and Brown 2002) and predator-prey dynamics also play a role (Ellertsen et al. 1981). Larval cod in the wild typically experience temperatures between 5 and 7 °C (ICES 2005; Folkvord 2005 and references within), but will grow rapidly at temperatures of 14 and 16 °C (Otterlei et al. 1999).

The location and timing of spawning by Gilbert Bay cod and physical characteristics including bathymetry and seasonally structured water column is likely to affect egg dispersal. Because these features support a localized population, they could foster local adaptation. The inference of local adaptation promoting low connectivity (reduced exchange of individuals with other populations) through both location and time of spawning is further supported by studies of cod movement (Chapter 4) and genetic analysis (Bradbury et al. 2010). This 14-year study examines the location and timing of Atlantic cod spawning as well as early development and local oceanographic conditions

in Gilbert Bay. Specifically it addresses how these factors influence the retention of eggs and larvae near the spawning area in Gilbert Bay.

## 3.3 METHODS

### 3.3.1 Study area

Gilbert Bay is a shallow-water, low-gradient, sub-Arctic fjord, located on the southern coast of Labrador 52°35'N 56°00'W (Figure 3.1) measuring ~ 28 km in length and 1-2.5 km in width with a total area of 60 $km^2$. Ice covers Gilbert Bay from December until early May. Two large rivers at the head of Gilbert Bay, Gilbert River and Shinneys River, influence the oceanographic characteristics in the area, particularly during spring. The 132-km long Gilbert River drains a watershed of 642 $km^2$ in contrast with the shorter 76-km long Shinneys River which drains a 313 $km^2$ area (Anderson 1985). A long-term river monitoring station on the Alexis River provides information on timing of the spring freshet in this region of Labrador. The Alexis River runs parallel to Shinneys and Gilbert Rivers; as little as 5 km separate the head waters of these rivers.

A multibeam survey of the seabed features of Gilbert Bay in 2003 (Morris and Power 2004) provided data used to describe benthic features in the area. Data from this survey were extensively analyzed and ground-truthed by Copeland et al. (2011a, 2011b). The complex bathymetry, which is important to the exchange of water in the bay, spans seven basins along the length of the fjord separated by six sills (Copeland et al. 2011a). The

basins range in depth from 32 m near the head of the bay to 163 m at the mouth, and the sills range in depth from 4 m to 65 m. MPA zone 1a, an area known as The Shinneys, branches to the southwest of the Main Arm of Gilbert Bay, where a narrow channel and shallow sill at 4 m depth restricts exchange with the Main Arm.

Copeland et al. (2011b) differentiated five habitat types based on multibeam substrate analysis and ground truthing. Much of the mapped fjord is shallower than 30 m with a mean depth 33.2 m throughout. The substrate is 41% gravelly mud, 38% muddy gravel, 10% sandy mud, 10% mud, 8% coralline-algae-encrusted gravel, 4% sandy gravel and large kelp (Laminaria spp.) and sea grasses are effectively absent (Copeland et al. 2011b).

### 3.3.2 Sampling

Vertical measurements of the water column including conductivity, temperature, and depth (CTD) were conducted during the spring melt (late May – early June), which coincides with the Gilbert Bay cod spawning season, and in mid-summer (early August). CTD data were collected using a Seabird Electronics Inc. Seacat SBE 19- 01 probe, and YSI hand held salinity probe.

Continuous water temperature data were collected from temperature loggers (Vemco mini-log T, ± 0.2 °C accuracy) positioned at 2-3 meters and 7-8 meters depth in zone 1a. Although data collections were consistent most years, lost or malfunctioning probes resulted in incomplete data in some years.

Ichthyoplankton sampling was conducted primarily during two periods: late May – early June (spring) and again during early August (summer) of each year (except 2003). During 1999 sampling was also conducted in late June (Morris and Green 2002). Sampling was conducted during the morning (7:30 - 10:30 am); however, during August additional sampling was conducted near dusk (6:30 - 8:30 pm). Morris and Green (2002) describe the protocol used to sample eggs and pelagic juvenile cod, which was followed throughout the time series. Data described by Morris and Green (2002) were also included in this analysis to extend the time series. Ichthyoplankton samples were collected using a 1-m diameter ring net with 333 μm mesh towed horizontally for 15 minutes, while maintaining a constant boat speed to sample a fixed depth. Boat speed was monitored using a hand held Global Positioning System (Garmin 60 CSx). Egg sampling was typically conducted at speeds of 3.8, 2.4, and 1.7 km/hr which sampled depths of 1-2 m, 4-5 m, and 7-8 m respectively, dependant on length and angle of the towrope. Different tow speeds were necessary to maintain the net at a specific depth. Pelagic juvenile sampling was only conducted at 1-2 m with typical boat speed of 3.8 km/hr. In 2009, sampling depth was validated to ± 1 m using a depth gauge which showed that the deepest tows (7-8 meters) varied between 7 and 11 m. Some sampling error was expected, particularly at greater depth, because of small fluctuations in boat speed and during net deployment and retrieval. The same locations were sampled each year, fixing egg samples in 5% formalin and preserving larvae in 95% ethyl alcohol. In the laboratory, eggs were characterized using the four part egg staging scheme of Markel and Frost (1985). For larger samples a Motoda splitter was used to subsample a smaller volume containing at least 300 eggs, which were then counted and identified to

development stage. Egg sampling within Gilbert Bay was conducted to identify their primary location in the water column (deep versus surface layer), their geographic location (Shinneys and the Main Arm (zone 1b, zone 2 and zone 3)), and their developmental stage. The concentration of eggs in the water column was estimated from the expected sample volume associated with a given tow distance. Differences in egg concentration were compared between locations using an unpaired two-tailed Student's t-test with unequal sample size and assuming equal variance.

Morphometric transformation of Atlantic cod from larvae to the early juvenile stage occurs at sizes greater than 20 mm (Fahay 2007). Standard lengths of pelagic juvenile cod were measured to within 0.1 mm using Vernier calipers under a dissecting scope. To compare growth rates of Gilbert Bay cod with other studies, standard lengths were converted to dry weights using:

$$\ln DW = -9.38 + 4.55 \ln SL - 0.2046 (\log SL)^2$$

where SL denotes live standard length (mm) and DW denotes dry weight (mg) (Folkvord 2005). The following equation was used to account for shrinkage in 95 % ethanol:

$$\text{Log SL} = 0.056 + 0.978 \text{logPSL}$$

where PSL denotes preserved standard lengths. Parameters were obtained from Otterlei (1999).

The duration of the egg stage was estimated using temperature-dependent development rates described by Page and Frank (1989) and constants reported by Geffen et al. (2006).

$$H = a\,(T+2)^{b}$$

where T denotes observed water temperature in Gilbert Bay and constants a = 74.131 and b = -0.82.

The estimated hatching period was used to calculate an age-range for pelagic juvenile cod sampled in August in order to estimate specific growth rates. Otoliths (lapillus) from nine larval cod sampled in 1999 were aged in days by experienced technicians in order to corroborate the estimated specific growth rates.

The specific growth rates of Gilbert Bay cod was compared to a temperature-dependent growth model by Folkvord (2005).

$$SGR = c_0 + c_1 \ln DW + c_2 (\ln DW)^2 + c_3 (\ln DW)^3$$

with $c_i = a_i + b_i$Temp, where Temp denotes the average daily temperature (°C) and ln DW denotes the natural log of the estimated larvae dry weight (mg) on a given day. Average daily temperatures from Gilbert Bay collected at 2-3 meters depth were used,

corresponding to the depth at which larval cod were sampled. The growth model by Folkvord (2005) was used to support predictions of hatching dates based on temperature-dependent egg development rates, and to validate the specific growth rates observed for pelagic larvae and juvenile cod. Previous work demonstrated an approximately linear temperature effect on growth (Otterlei et al. 1999).

## 3.4 RESULTS

During spring the melting winter snowfall accumulations from the surrounding watershed produced a strong seasonal increase in freshwater runoff each year (Figure 3.2), referred to hereafter as the spring freshet. During spring, a surface layer of low-salinity water affected the upper 3-5 meters of the water column; however the stratification observed each spring became less prominent during summer (Figure 3.3).

Surface water temperatures are subzero during winter, but increase rapidly after ice leaves the bay in May, and by mid-summer surface temperatures reach 15-16 °C (Figure 3.4). However temperatures increased earlier in years when the ice melted earlier and daily water temperatures at 2-3 m were more variable than temperatures recorded at 8 m (Figure 3.5). At 8 m depth, which was the median depth for hook and line sampling (see Chapter 2), water temperatures exceeded 0 °C from early June until late December. The average cumulative degree days (i.e. summation of daily water temperatures exceeding 0 °C) at 8 m, a typical sampling depth for Gilbert Bay cod, was ~1100 (Figure 3.6).

During the egg and larval period in Gilbert Bay water temperature, density, and egg concentrations varied widely over a small depth range (Figure 3.5). During the period of egg development and larval growth, from mid-May until early August, water temperatures averaged 5 °C warmer at 3 m than at 8 m depth. Between early June and early August, temperatures at 2-3 m depth ranged from 5 to 14 °C, and at 8 m from 1-10 °C, (Figure 3.4). However, eggs were not exposed to high surface temperatures because they were confined to a deeper, denser layer (> 5 m) of the water column. The highest concentrations of cod eggs occurred at or below the bottom of the pycnocline (defined as a 10% change in density with a 1 meter change in depth; after Boyra et al. 2003), at depths >3 m (Table 3.1). No Atlantic cod eggs (nor other fish eggs) were collected during late May and early June sampling in depths less than 3 m; eggs were only collected from below the pycnocline. Maximum concentrations of cod eggs were sampled between 4 and 10 meters depth depending on sampling year (1998-2011).

Atlantic cod eggs were sampled at higher concentrations in zone 1a than in the Main Arm of Gilbert Bay ($P < 0.001$, two-tailed t-test assuming equal variance) (Table 3.1). Stage 1 cod eggs dominated in early June of each year at both sampling locations, with relatively few stage 2 eggs. Based on reported development rates for Atlantic cod eggs, spawning in Gilbert Bay likely began in May during the 14-year study. Consistent observation of predominantly stage 1 eggs in early June and only pelagic juveniles in early August suggests that all egg development in Gilbert Bay cod occurs between May and late June.

Ichthyoplankton sampling conducted during the first week of August collected pelagic juvenile cod each year from 1998-2011; except for 2003 when no sampling was done. Early August plankton tows sampled only pelagic juvenile cod with an average SL of 24.9 mm (Figure 3.7). A similar size range (15-40 mm SL) was observed in pelagic juveniles sampled in early August from 1998 to 2011 (Figure 3.7). Using available temperature data, and assuming most eggs hatch between June 15-30$^{th}$ based on temperature-dependant egg development rates and a median peak in pelagic juvenile cod numbers on the August 5$^{th}$ sampling date, suggested an average specific growth rate between 0.49 – 0.71 mm per day.

Counts of daily growth increments for nine pelagic juveniles (15.0 – 43.5 mm SL) sampled in early August 1999 were estimated at 35 – 58 days old. Presumably, most fish within this size range likely hatched in June given observed annual water temperature and egg staging data.

Annual average densities of pelagic juvenile cod sampled in early August ranged from 0.2 – 7.0 cod per tow from 1998-2011. Higher concentrations of juveniles were present in zone 1a than the Main Arm of Gilbert Bay for all years except 1998, and 2005 (Figure 3.8). Concentrations of pelagic juvenile cod were very low in several recent years, 2007, 2008, 2010, and 2011 in particular. Sampling in zone 1a during morning hours (7:30-10:30 am) yielded only one third as many fish as near dusk (6:30-7:30 pm) sampling.

## 3.5 DISCUSSION

In Gilbert Bay, most Atlantic cod overwinter and spawn at the same location - in MPA zone 1a (Chapter 4) – spawning occurs during a relatively short period in the spring. During the spring freshet, zone 1a comprises a highly stratified estuary (Pickard and Emery 1982), where freshwater runoff produces buoyancy driven currents flowing seaward, mixing as runoff enters the Labrador Sea. Cod eggs were confined beneath the low salinity surface layer, likely because of their buoyancy and adult spawning depths (Sundby 1983; Norcross and Shaw 1984 and references therein; Sundby 1991). Gilbert Bay surface density during spawning was less than 10 $kg{\cdot}m^{-3}$, and increased to >25 $kg{\cdot}m^{-3}$ at 7 m. In general, Atlantic cod eggs and early stage larvae are found at densities of 22-26 $kg{\cdot}m^{-3}$ (Saborido-Rey et al. 2003; ICES 2005), which would limit cod eggs to depths that would limit dispersal from zone 1a so that a large proportion would be retained. Neutrally buoyant eggs between 22 and 26 $kg{\cdot}m^{-3}$ would occur at depths of 5 m or more below the partially mixed surface layer and below the sill depth separating zone 1a from the Main Arm. Despite the retention of eggs and larvae, the abundances of pelagic juveniles did not correlate with abundances of older year classes (2-5 yrs) sampled using hook and line (Chapter 2). One year old cod were not sampled with hook and line or during ichthyoplankton tows.

Many populations of Atlantic cod spawn over a period of 2-3 months or more (Pinsent and Methven 1997; ICES 2005). In Newfoundland and Labrador waters, inshore cod aggregations in Placentia Bay and Smith Sound spawn between April and July, and even until August (Bradbury et al. 2000; Knickle and Rose 2010; Morris personal

observations). The Gilbert Bay cod population completes spawning, egg development and hatching during May and June, beginning when water temperatures increase above 0 °C and coincident with the development of the spring freshet. After hatching in early summer, larvae and pelagic juveniles grow during the warmest and (presumably) most productive time window for the Gilbert Bay water column, in conditions generally favorable for the development and growth of Atlantic cod larvae and pelagic juveniles (Folkvord 2005; Geffen et al. 2006). These conditions likely occur at the beginning of the short growing season in Gilbert Bay, though specific data on the timing of spring bloom are lacking for Gilbert Bay.

Despite the small spawning population in Gilbert Bay (Morris et al. 2003), and relatively small-bodied fish (Chapter 2), egg concentrations during spawning were high. The short spawning season, restriction of eggs beneath the low salinity surface layer, and bathymetric concentrating mechanism all contribute to the retention of eggs within a narrow vertical depth range at the spawning site. At many other locations the reported concentrations of Atlantic cod eggs were lower than those in Gilbert Bay. In Placentia Bay, Bradbury et al. (2000) reported < 10 eggs·m$^{-3}$, in Trinity Bay Knickle and Rose (2010) reported <1 egg·m$^{-3}$, on the northeast Newfoundland Shelf Anderson and deYoung (1995) reported densities less than 0.1 egg·m$^{-3}$, and in the Gulf of St. Laurence Ouellet (1997) found egg densities of <1 egg·m$^{-3}$. The Arcto-Norwegian spawning ground off Lofoten, Norway, is exceptional with egg concentrations of 300 eggs·m$^{-3}$ (ICES 2005). In the coastal areas of Norway, Knutsen et al. (2007) reported egg densities of <3 eggs·m$^{-3}$ in many fjords (n=20), and concluded that higher egg densities inside

sheltered fjords provided evidence of an egg retention mechanism, as evidenced in Gilbert Bay, associated with sills near the fjord mouths that contributed to population structure (Espeland et al. 2006).

Bay-scale population structure has been hypothesized in Atlantic cod (Ames 2004; Myers et al. 1997; Robichaud and Rose 2004), likely driven by physical environment and behaviour of individuals during early life stages and as adults. Studies of coastal Atlantic cod in Norway (Espeland et al. 2007; Olsen et al. 2008; Ciannelli et al. 2010 and Knutsen et al. 2007) suggest an evolutionary advantage to spawning in the inner portion of some fjords, where egg flushing from the fjord is less likely. Collectively these studies contend that small-scale egg retention explains consistently high concentrations of eggs inside the fjord and ultimately the maintenance of local population structure over time. Spatially structured adaptive traits, which might include spawning location and adult site fidelity, indicative of local adaptive evolution, mirror this population structure (Olsen et al. 2008; Ciannelli et al. 2010).

The highly stratified outflow plumes of estuaries provide strong stability that dissipates wind-induced turbulence within the top few meters (Boyra et al. 2003). In Gilbert Bay, temperatures at shallow depths (3 m) near the pycnocline vary more than at slightly greater depths (8 m), suggesting there are greater effects of wind and wave turbulence than at greater depths, where the eggs occur. Mechanical stress can contribute to fish egg mortality during development (Holmefjord and Bolla 1988; Caberoy and Quinitio 1998; Hilomen-Garcia 1998). Rollefsen (1929), as reported by Sundnes et al. (1965), indicated

that mechanical forces can easily destroy cod eggs, and suggested that strong wind and waves might therefore diminish spawning success. Noting that much of the spawning area in Gilbert Bay is less than 30 m deep, the surface layer of relatively fresh water in Gilbert Bay may help to protect Atlantic cod eggs (located just 3-5 meters below the surface) from physical damage during sensitive periods of development.

Temperature is perhaps the single most important determinant of growth rates of early life history stages of fish in the wild (Houde 1989; Blaxter 1991; Trudgill et al. 2005; Neuheimer and Taggart 2007). Several studies report on temperature-dependent cod egg development (Geffen et al. 2006 and references therein) and larval and pelagic juvenile Atlantic cod growth (Folkvord 2005 and references therein). In Gilbert Bay, temperatures vary widely within the upper 10 m of the water column after ice breakup occurs and before peak summer temperatures. This period encompasses Atlantic cod development for Gilbert Bay from spawning until the pelagic juvenile stage. Although the temperature history experienced by individual eggs and larvae was not known, the warm temperatures that favour rapid egg development occur for only a limited period in Gilbert Bay.

The growth of larval and pelagic juvenile cod correlates with temperature (Otterlei et al. 1999; Folkvord 2005 and references within). Laboratory studies show maximum weight-specific growth rate potential exceeding 25% per day for larval cod fed in excess at temperatures of 14 and 16 °C for Norwegian coastal and Northeast Arctic cod, respectively (Otterlei et al. 1999). Van der Meeren et al. (2001) reported growth rates of 18.1-22.3% per day (dry weight) for cod reared for 46 days as temperature increased

from 7 to 16 °C, which is comparable to rates in Gilbert Bay. Gilbert Bay cod would require 40 days to attain the observed average size of 24.9 mm (~24 mg dry weight), assuming 20% growth (dry weight) per day. Interestingly, cod larvae sampled in the wild apparently grow at rates close to their maximum capacity given the water temperature they experience (Folkvord 2005), potentially reflecting the importance of growing fast during the larval stage (Brown et al. 1989).

Compared with offshore habitats, development of early life history stages in coastal areas may result in higher survival because of decreased predation and higher growth rates associated with higher prey densities (Frank and Leggett 1982; Taggart and Leggett 1987a; 1987b; Pepin and Shears 1995). Zooplankton, particularly copepods and copepod eggs including those from *Calanus finmarchicus* and the genera *Acartia* and *Temora*, occur in high densities in Gilbert Bay (Morris unpublished data), and can be important food for larval cod (ICES 2005 – Ireland stock). The highest concentrations of Atlantic cod larvae on Western Bank, Nova Scotia coincided with gyre-like water masses and their associated frontal features at which high copepod concentrations (6500 individuals·$m^{-3}$) were measured (McLaren and Avendano 19x95). Prey densities (3900-7900 individuals·$m^{-3}$) were similar to those sampled in Gilbert Bay during 2001 (Morris unpublished data). Compared to temperate waters, sub-arctic coastal estuaries have a shorter period of highly productive waters when food limitation may be unlikely.

Genetically, the Gilbert Bay cod population has been reported to be the most distinctive population in the western Atlantic (Beacham et al. 2002; Ruzzante et al. 2000), at least

partly because of contemporary genetic isolation (Bradbury et al. 2010; Bradbury et al. 2011). Although environmental conditions that limit the dispersal of eggs and larvae may contribute to genetic isolation, adult movement patterns also play an important role in population connectivity and persistence of locally distinct populations. Gilbert Bay cod regularly intermingle with other Atlantic cod populations during feeding migrations, however, individuals separate during spawning. Localized physical features that reduce the distribution of early stages combined with active behaviour and site-fidelity through later life history stages could help to define population structure within the species through connectivity. The next chapter develops and tests hypotheses that support site fidelity and natal homing behavior of individual Gilbert Bay cod across years, to the same spawning area, which approaches 100% (Chapter 4).

## 3.6 CONCLUSIONS

The spawning behaviour, (location and timing) in concert with the physical characteristics of freshwater runoff and shallow sills, considered in tandem with behaviour of individuals at older life history stages, provides a framework to explain how the Gilbert Bay cod population maintains extremely low connectivity with other populations. This population provides a valuable addition to the intraspecific biocomplexity of Atlantic cod in the Northwest Atlantic. Identifying biocomplexity among wild populations informs applied ecological research and our understanding of the adaptive potential of fish populations and their contribution to intraspecific diversity.

The conservation and maintenance of adaptive diversity, which includes identifying divergence, is widely believed to play a critical role in the stability and persistence of populations and species (Hilborn et al. 2003; Schindler et al. 2010; Bradbury et al. 2012). Therefore, informed management decisions require better understanding of marine population connectivity and these ideas are explored further in Chapters 5 and 6. Gilbert Bay cod move in and out of the MPA into a much larger Atlantic cod management area, NAFO divisions 2J3KL, and this population may decline further (see chapter 5) in the absence of adequate protection measures that recognize metapopulation structure. Protecting important population structure will require additional protection specific to the Gilbert Bay cod population. Chapter 6 suggests that careful use of adaptive decision making in Marine Protected Areas could provide a central critical element of a prudent conservation strategy.

Table 3.1. Concentration and percentage of Atlantic cod eggs in each of 4 development stages that were sampled in zone 1a and Main Arm of Gilbert Bay. No eggs were sampled at 2 m depth near the surface. Maximum concentration (eggs·$m^{-3}$) of cod eggs sampled is indicated. Sampled concentration of eggs were significantly higher in zone 1a than the Main Arm of Gilbert Bay (P = 0.002, two tailed t-test assuming equal variance).

| Location | Date | Maximum conc. | Depth (m) | Developmental stages | | | | Tot. Tows |
|---|---|---|---|---|---|---|---|---|
| | | | | %St 1 | %St 2 | %St 3 | %St 4 | |
| zone 1a | 1 June 99 | 63 | 7 | 95 | 4 | 1 | 0 | 10 |
| | 3 June 01 | 65 | 5 | 93 | 5 | 1 | 0 | 6 |
| | 6 June 04 | 60 | 7 | 87 | 9 | 4 | 0 | 4 |
| | 1 June 05 | 23 | 4 | 94 | 6 | 0 | 0 | 4 |
| | 3 June 07 | 62 | 7 | 100 | 0 | 0 | 0 | 9 |
| | 7 June 08 | 36 | 10 | 95 | 3 | 2 | 0 | 7 |
| | 4 June 09 | 54 | 4 | 94 | 5 | 1 | 0 | 14 |
| | 2 June 11 | 90 | 5 | 94 | 5 | 1 | 0 | 7 |
| | | | | | | | | |
| Main Arm | 29 May 01 | 7 | 4 | | | | | 9 |
| | 5 June 07 | 5 | 5 | 97 | 3 | 0 | 0 | 3 |
| | 3 June 11 | 4 | 7 | 95 | 3 | 2 | 0 | 3 |

Figure 3.1. Map of the study area showing the Gilbert Bay MPA. Red denotes MPA zones 1a and 1b, yellow denotes zone 2 and green denotes zone 3.

Figure 3.1

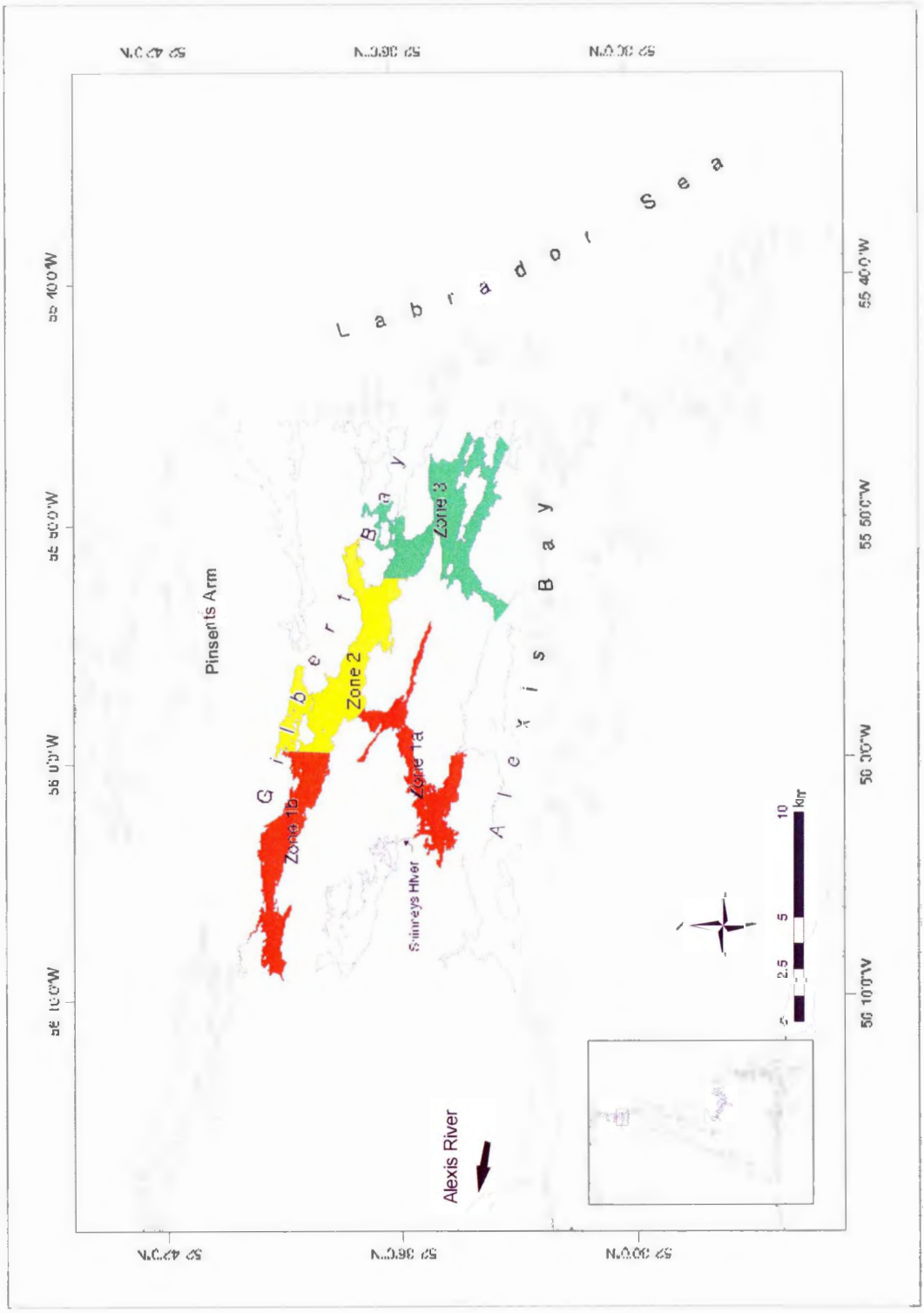

Labrador Sea
Gilbert Bay
Alexis Bay
Pinsents Arm
Zone 1a
Zone 1b
Zone 2
Zone 3
Skinneys River
Alexis River
10
5
2.5
0
km

Figure 3.2. April through August average daily discharge data for the Alexis River from 1978-2010. A prominent peak in runoff during the spring thaw lasted from mid April until late June. Data from 2006 and 2009 provide two examples of annual runoff; an early spring in 2006 and an 'average' year in 2009. Note low runoff between August and April.

Figure 3.2

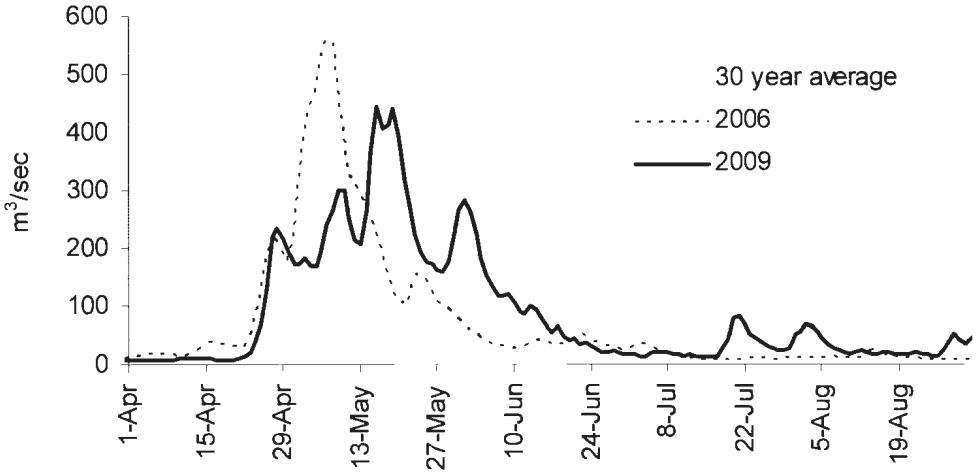

600
500
400
300
200
100
0
m3/sec
30 year average
2006
2009
1-Apr
15-Apr
29-Apr
13-May
27-May
10-Jun
24-Jun
8-Jul
22-Jul
5-Aug
19-Aug

Figure 3.3. Annual vertical profiles of water density in zone 1a and Main Arm of Gilbert Bay during spring and summer between 1999 and 2011. Data were not collected in all years.

Figure 3.3

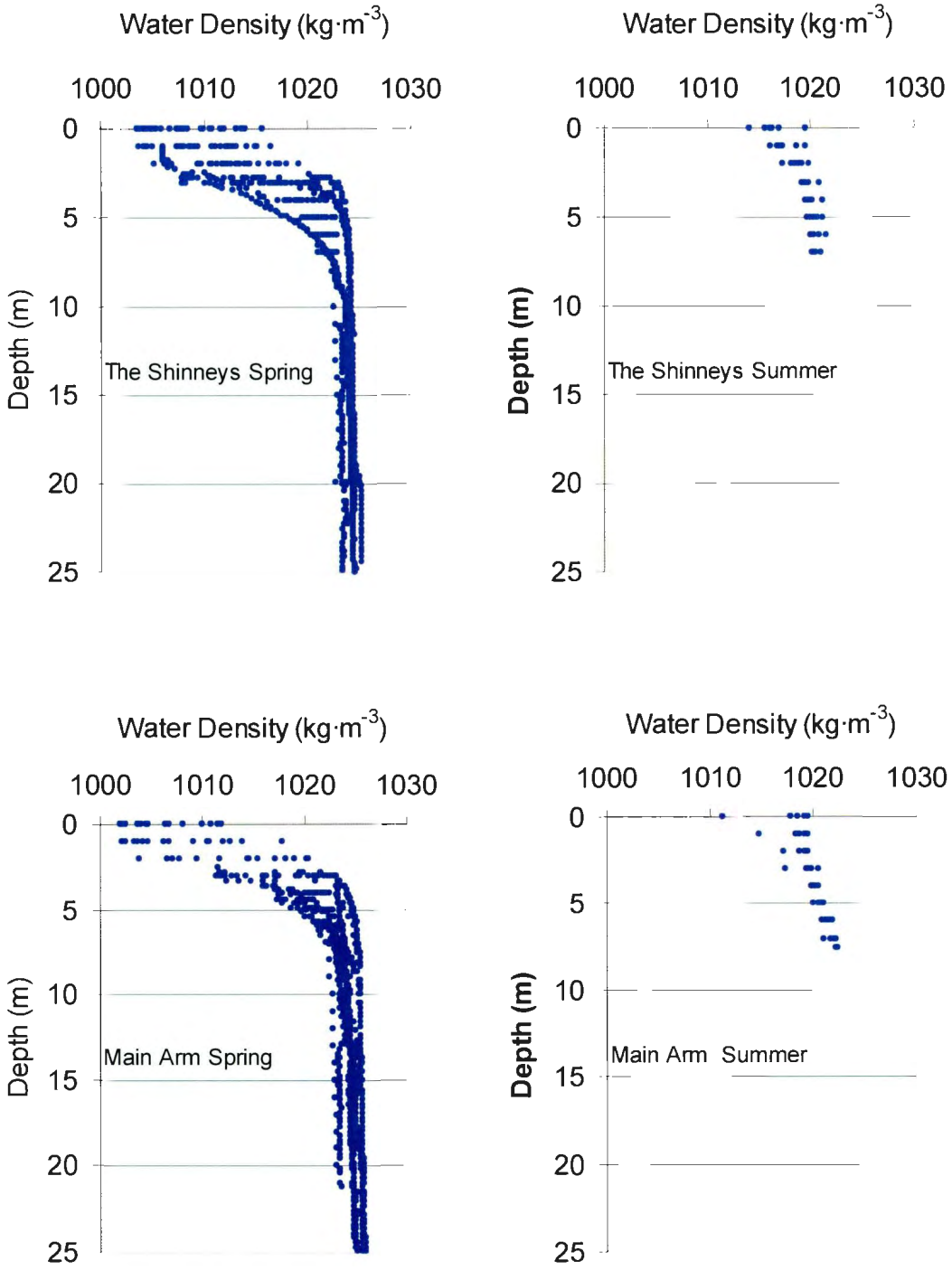

Water Density (kg·m-3)
1000
1010
1020
1030
0
5
10
15
20
25
Depth (m)
The Shinneys Spring
Water Density (kg·m-3)
1000
1010
1020
1030
0
5
10
15
20
25
Depth (m)
The Shinneys Summer
Water Density (kg·m-3)
1000
1010
1020
1030
0
5
10
15
20
25
Depth (m)
Main Arm Spring
Water Density (kg·m-3)
1000
1010
1020
1030
0
5
10
15
20
25
Depth (m)
Main Arm Summer

Figure 3.4. Annual mean daily water temperatures in zone 1a at 2-3 and 7-8 meters depth. Bottom panel represents average daily temperature at each depth from 1998-2010.

Figure 3.4

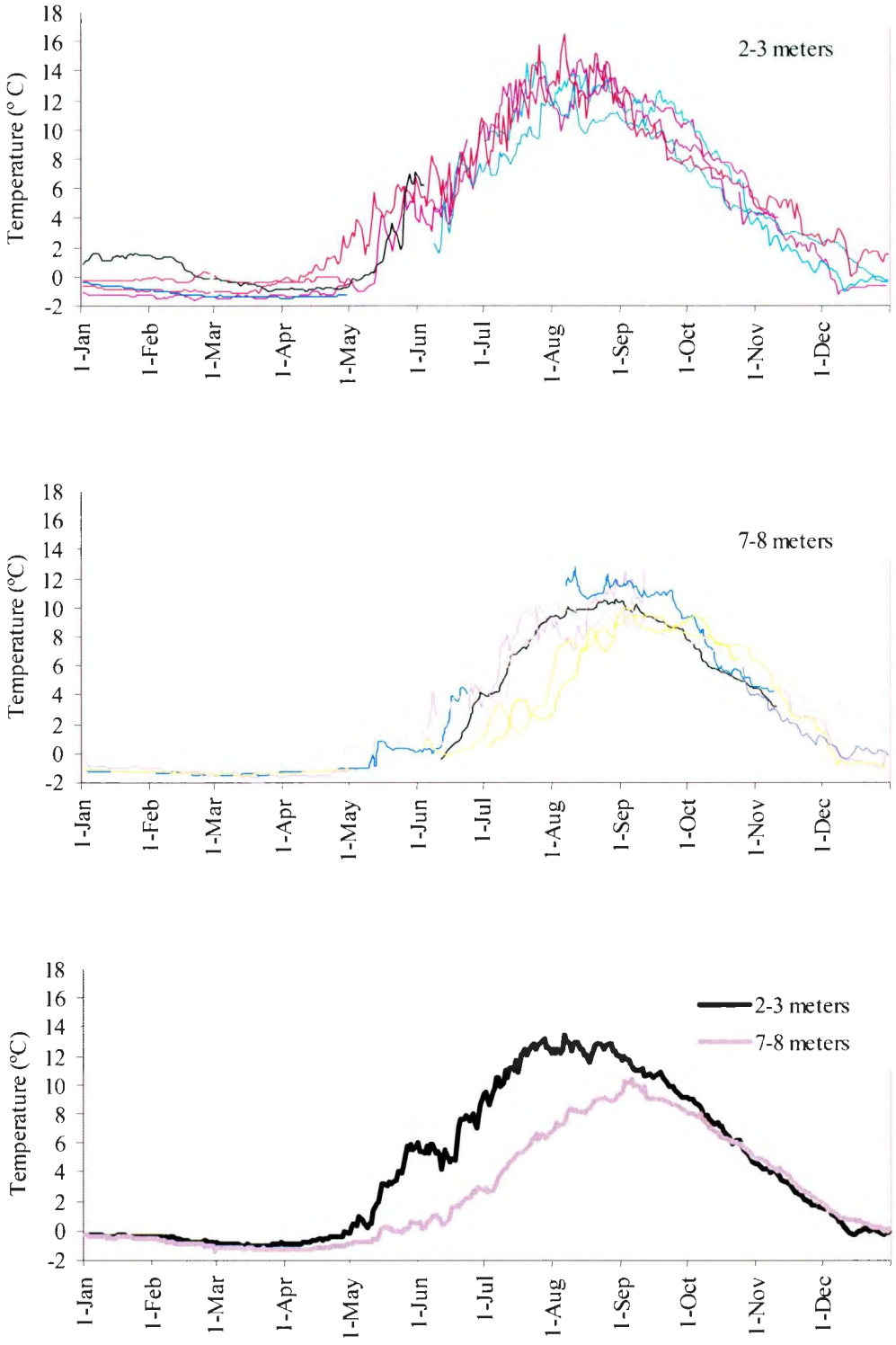

2-3 meters
Temperature (° C)
18
16
14
12
10
8
6
4
2
0
-2
1-Jan
1-Feb
1-Mar
1-Apr
1-May
1-Jun
1-Jul
1-Aug
1-Sep
1-Oct
1-Nov
1-Dec
7-8 meters
Temperature (°C)
2-3 meters
7-8 meters

Figure 3.5. Average daily water temperature at 2-3 and 7-8 meters depth in zone 1a, during the egg and pelagic larval development period from mid-May to early August. The bottom panel is the average temperature at each depth the entire time series.

Figure 3.5

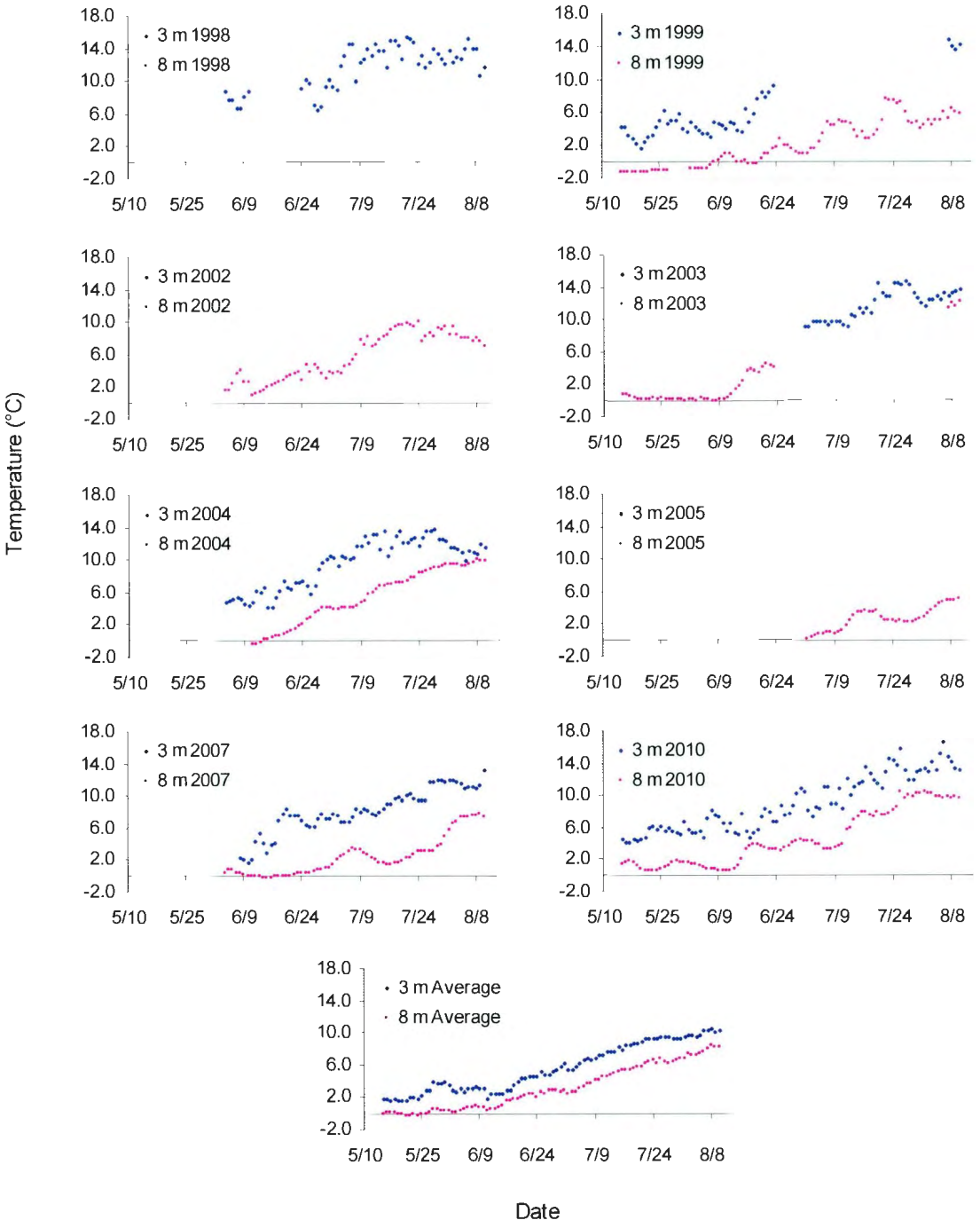

Temperature (°C)
18.0
14.0
10.0
6.0
2.0
-2.0
5/10
5/25
6/9
6/24
7/9
7/24
8/8
3 m 1998
8 m 1998
3 m 1999
8 m 1999
3 m 2002
8 m 2002
3 m 2003
8 m 2003
3 m 2004
8 m 2004
3 m 2005
8 m 2005
3 m 2007
8 m 2007
3 m 2010
8 m 2010
3 m Average
8 m Average
Date

Figure 3.6. Average cumulative degree days at 8 meters depth in zone 1a based on thermograph data collected from 1998-2011.

Figure 3.6

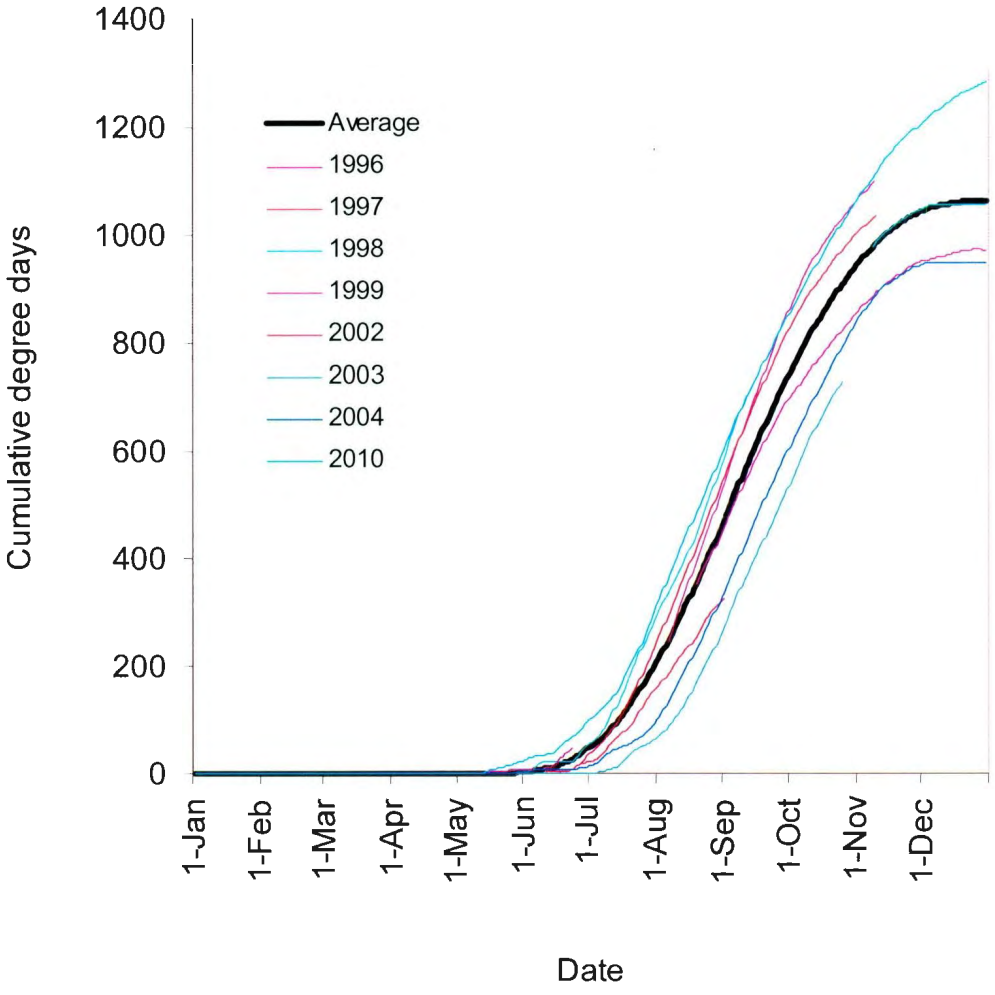

1400
1200
1000
800
600
400
200
0
Cumulative degree days
Average
1996
1997
1998
1999
2002
2003
2004
2010
1-Jan
1-Feb
1-Mar
1-Apr
1-May
1-Jun
1-Jul
1-Aug
1-Sep
1-Oct
1-Nov
1-Dec
Date

Figure 3.7 Average length of pelagic juvenile Atlantic cod sampled in zone 1a (95% CI) between 1-10 August each year. The number of fish sampled each year is indicated.

Figure 3.7

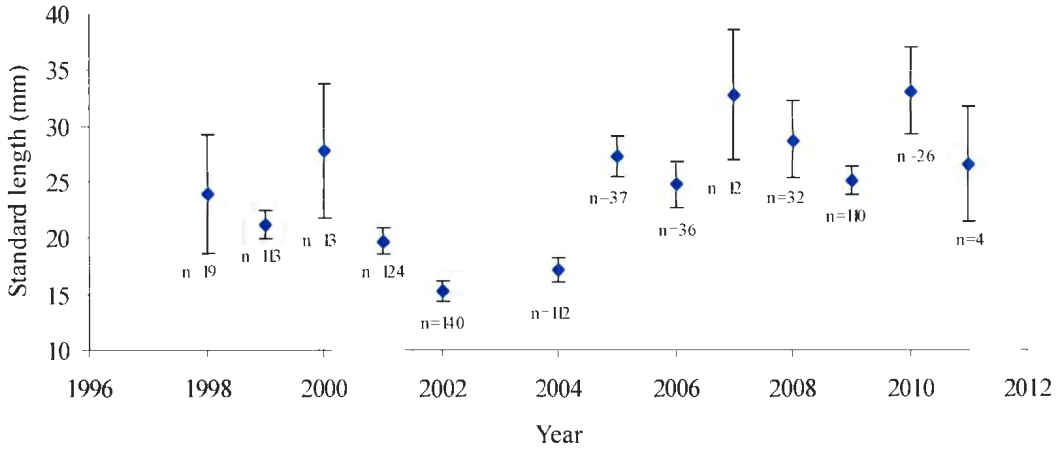
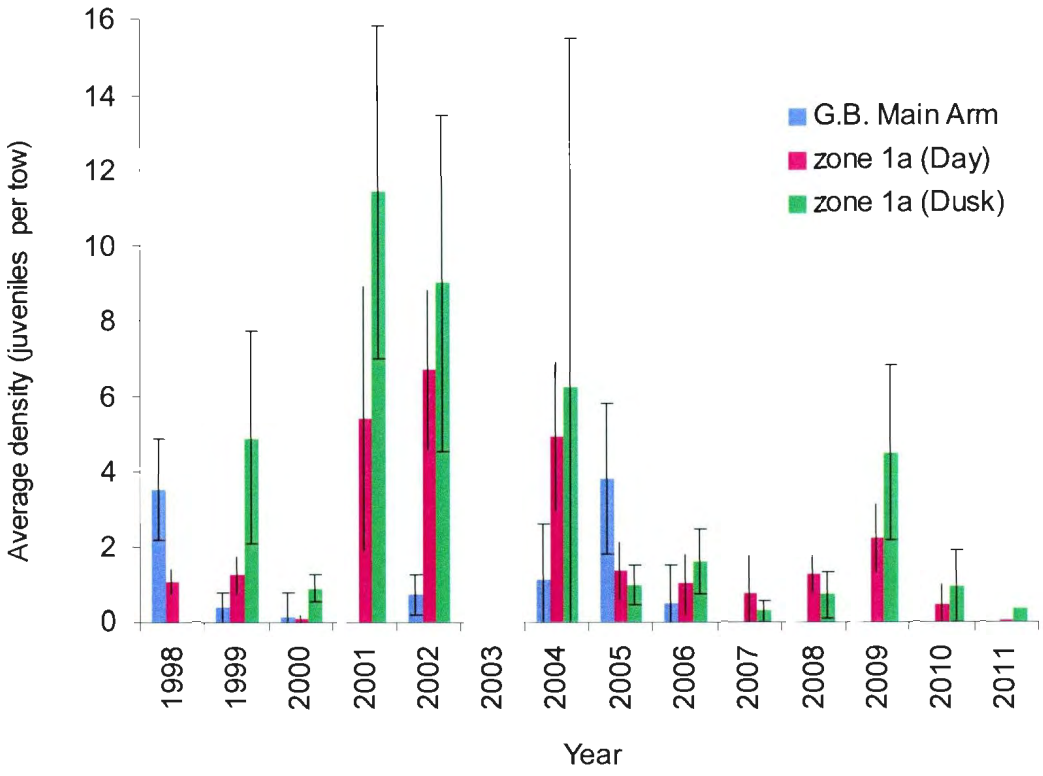

Standard length (mm)
40
35
30
25
20
15
10
1996
1998
2000
2002
2004
2006
2008
2010
2012
Year
n=19
n=113
n=13
n=124
n=140
n=112
n=37
n=36
n=12
n=32
n=110
n=26
n=4

Figure 3.8. Average number (95% CI) of pelagic juvenile Atlantic cod caught per tow in zone 1a and the Main Arm of Gilbert Bay. Sampling was conducted during the day in zone 1a and Main Arm (7:30-10:30 am) and also near dusk (6:30-8:30 pm) in zone 1a.

Figure 3.8


Average density (juveniles per tow)
16
14
12
10
8
6
4
2
0
G.B. Main Arm
zone 1a (Day)
zone 1a (Dusk)
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

## Chapter Four

## Site fidelity and homing behaviour of Atlantic cod within a sub-arctic Marine Protected Area; necessity of experience for navigation and migration

### 4.1 ABSTRACT

To evaluate adult and juvenile contributions to connectivity of Atlantic cod and MPA effectiveness, the movement patterns of cod from the Gilbert Bay Marine Protected Area were studied using external tagging and acoustic telemetry tracking. Recaptures of 314 of 8213 externally tagged cod at the spawning area demonstrated site specificity in most individuals. These were typically recaptured within 500 m of the initial tagging location for time periods up to nine years after release. An array of moored acoustic telemetry receivers showed over a seven year period (2005-2011) that of the Gilbert Bay cod that migrated, 93% of adults (58 – 81 cm TL) and 70% of the immature (34-38 cm TL) homed to a specific overwintering and spawning area each year. The home range of the Gilbert Bay cod population encompasses an area within 40 km of the population's core area. Understanding home range and homing behaviour enabled us to investigate the role of experience in migration using transplant and tracking experiments. Immature and adult ultrasonically tagged cod transplanted to areas outside an observed home range did not return to the home site. In contrast, fish transplanted within the known home range returned rapidly, suggesting that experience facilitates cod navigation and migration. If experienced adults are to conduct successful migratory feeding behaviours in order to improve growth and reproduction, then management strategies should consider the need

to maintain a demographic structure that includes older individuals that can facilitate learning of migration and thus assist in successful recruitment and stock recovery.

## 4.2 INTRODUCTION

Until recently the world's oceans were considered an area of broad-scale mixing, however, recent findings of small, spatially discrete populations prompted interest in marine connectivity research (Warner and Cowen 2002; Palumbi 2003; Dawson et al. 2006; Almany et al. 2007; Cowen et al. 2007; Jones and Srinivansan 2007). Increasing evidence has shown limited dispersal, site-specific and homing behaviour of juveniles and adults, and genetic differentiation often related to oceanographic conditions that define connectivity patterns (Jones et al. 1999; Warner et al. 2005; Levin 2006; Botsford et al. 2009; Chapter 2). Spatial and temporal differences in environmental characteristics that influence survival, growth, and reproduction can also affect life history strategies, including migratory behaviour in mobile organisms (Taylor and Taylor 1977), which can therefore affect population connectivity.

Wide dispersal associated with any one life history stage can potentially eliminate population structure that might be expected from the limited dispersal of other stages (Palumbi 1994; Bohonak 1999). Multiple studies document sub-population structure of Atlantic cod across a wide range of environmental conditions, where some sub-populations exhibit higher connectivity than others (Ruzzante et al. 2000; Beacham et al. 2002; Smedbol and Wroblewski 2002; Bradbury et al. 2011). In many instances, early life stages are identified as primary drivers of population structure because spawning

locations interact with oceanographic currents, wind, and bathymetry to determine the dispersal of Atlantic cod eggs and larvae (Pepin and Helbig 1997; Knutsen et al. 2007). For example, Atlantic cod eggs spawned in offshore areas are expected to disperse widely compared to those spawned in sheltered fjords (Pepin and Helbig 1997; Knutsen et al. 2007; Chapter 3).

Movements at older life history stages, such as the juvenile and adult stages, can also influence population connectivity. Previous studies of juvenile cod (<35-40 cm TL) movement suggest limited dispersal at this life history stage (Cote et al. 2003; Clarke and Green 1990). When Atlantic cod approach sexual maturity however, large portions of a population can exhibit an annual migratory behaviour (Templeman 1974). Thus, migration can interact with the dispersal of early life history stages, to influence population structure (Skjaeraasen et al. 2011; Svedang et al. 2007).

Migrations of Atlantic cod populations range from hundreds to only a few kilometers (Templeman 1974; Bergstad et al. 2008; Robichaud and Rose 2004; Skjaeraasen et al. 2011). On the one hand, offshore Atlantic cod populations inhabiting the continental shelves of Canada (Northeast Newfoundland Shelf and the Grand Banks) and Barents Sea cod off the coast of Norway undertake the most extensive migrations between feeding and spawning grounds (Templeman 1974; Bergstad et al. 1987; Rose 1993; Taggart 1997). Inshore populations, on the other hand, have migrations often limited to individual bays and fjords. Such populations are common on both sides of the Atlantic (Ames et al. 1997; Ruzzante et al. 2000; Knutsen et al. 2003; Ames 2004). Homing to specific

spawning sites appears to be a common element of Atlantic cod life history (Green and Wroblewski 2000; Robichaud and Rose 2001; Svedang et al. 2007), despite spatial overlap of populations during non-spawning periods. "Homesite" as used here refers to the particular locality with which an animal associates (termed "localization" by Scott 1958), and "homing" refers to the return of an animal to a place formerly occupied rather than to other equally probable places (Gerking 1959). Spawning sites are often within core areas, which are those areas used more frequently than any other areas and that probably also contain homesites and refuges (Burt 1943; Kaufmann 1962; Ewer 1968).

Early genetic evidence from small Atlantic cod populations by Ruzzante et al. (2000) and Hutchinson et al. (2001) showed that reproductive isolation can exist at bay scales, which are considerably smaller scales than previously thought. Since then, many studies identified small-scale genetic variability (Knutsen et al. 2003) and even suggested local adaptation among Atlantic cod populations (Olsen et al. 2008; Bradbury et al. 2012). Multiple studies of Atlantic cod populations associated with inshore features such as bays and fjords show that sills, currents, restricted passages, and island archipelagos that help in egg and larval retention and separation of spawning grounds often characterize the geography of these discrete populations (Bradbury et al. 2000; Knutsen et al. 2003; Espeland et al. 2007; Knutsen et al. 2007; Ciannelli et al. 2010; Knickle and Rose 2010; Skjaeraasen et al. 2011; Chapter 2). Although these conditions limit dispersal of early life stages, the behaviour of juvenile and adult stages also help maintain persistent, locally distinct populations. The mechanisms through which individual adult Atlantic cod maintain discrete population structure remains poorly known.

Natal homing and spawning-site fidelity are common in Atlantic cod populations (Rose 1993; Green and Wroblewski 2000; Morris and Green 2002; Robichaud and Rose 2004; Wright et al. 2006; Svedang et al. 2007; Knutsen et al. 2007; Ciannelli et al, 2010; Skjaeraasen et al. 2011) but the mechanism(s) remain poorly understood. Rose (1993) speculated that learning contributes to migration and opportunities to feed on capelin. Historically, the behaviour of offshore northern cod was characterized by an inshore summer feeding migration as offshore spawning and post-spawning aggregations moved shoreward to feed on capelin (Templeman 1974; Rose 2007). However, migration can be energetically costly, and some researchers speculate that selection in some species reduces feeding migration distances to an area within which necessary energy requirements can be met (Finstad and Hein 2012). For example, inshore Atlantic cod populations could access capelin or other food sources in relatively productive coastal areas with much shorter migration distances than offshore populations. Nonetheless, the factors affecting an individual's decision to migrate and navigational mechanisms involved remain poorly understood.

Adult behaviour could play an important role in maintaining discrete populations, including spawning behaviour (Chapter 3) and also through site-specific natal homing. Information on natal homing is critical to understanding the mechanism of population isolation and the efficacy of management strategies such as Marine Protected Areas (MPAs). Based on earlier work by Green and Wroblewski (2000) and Morris and Green (2002), more recent observations of population decline (Chapter 2) and consistency in the

location and timing of spawning in Gilbert Bay (Chapter 3), it was decided that more information on juvenile and adult cod was needed in order to improve MPA effectiveness. The goal of this study was to establish the degree to which juvenile and adult cod in Gilbert Bay exhibit site fidelity and contribute to population isolation, and thus MPA effectiveness.

This study was designed with two objectives. First, to describe migration timing and distance, and the size at which Gilbert Bay cod commence migration. The second objective was to build upon these observations to formulate and test hypotheses related to the role of experience that Gilbert Bay cod use to home. If experience were important to migration, then individuals from local populations would be incapable of returning from distances outside the population's home range because they lacked previous experience doing so. The experimental hypothesis is that Atlantic cod transplanted to an area within a known home range would return to the home site, whereas those transplanted outside their home range are less likely to return. Telemetry work on small cod (33-34 cm TL) by Morris et al. (2007) suggested that the home range of this size group of fish spans less than 5 km, and tracking data from the current study defined the home range of larger fish.

## 4.3 METHODS

### 4.3.1 External Tagging

Annual tagging of cod in Gilbert Bay with external Floy® tags began in 1998 and since then some 8213 individuals have been marked, the methods were previously described by

Morris and Green (2002). Since then additional data have been collected during 20 subsequent field trips to Gilbert Bay during 2002-2011. Briefly, sampling was conducted from small boats, between 4 and 7 m in length, twice each year; first during late May-early June (spring) and again in early August (summer). Healthy fish larger than 30 cm, were marked with an external individually numbered tag (Floy® t-bar tag) and released at the location of capture. Any recaptured cod with an external tag from previous tagging were sacrificed; however, recaptures per trip rarely exceed 20 individuals. Sacrificed fish were measured and, when sea conditions permitted, weighed before removing otoliths, identifying stomach contents, and estimating gut fullness. Fish were captured by angling at 33 sampling locations in zone 1a during each trip. Sampling sites averaged 2 hectares in size with spacing from 500 to 7500 meters apart within zone 1a. Most fishing locations were initially selected based on fish availability, and generally ranged from 5-10 m deep. Occasionally, sampling was conducted outside zone 1a, in Gilbert Bay and coastal areas, but Atlantic cod catch rates were very low in these areas during spring, and effort was limited by time constraints.

### 4.3.2 Internal tagging

Atlantic cod were caught for ultrasonic tagging from 2005 to 2009 (Table 4.1) in depths of 5-15 m using a straight one ounce fishing lure (Gibbs Minnow Jig™) on a handline. During surgery, fish were maintained in a wet trough, and covered with a cold wet cloth to reduce temperature-related stress. An ultrasonic transmitter was inserted into the body cavity through a 2-cm long incision along the abdomen, approximately 6 cm anterior to and above the vent. The incision was closed with 2 or 3 non-absorbable silk sutures

(Sofsilk™ Tyco Healthcare) after a total handling time of less than 2 minutes. Fish were briefly (generally less than 5 minutes) allowed to recover in a holding container, with water pumped from the depth at which the fish was caught, before release. Tagging procedures followed standards and guidance provided by the Canadian Council on Animal Care, and approved protocol was obtained from the Northwest Atlantic Fisheries Centre Animal Care Committee and Memorial Universities Animal Care Committee each year during the study.

The experimental protocol used to tag Gilbert Bay cod included two size groups and two release types. Ultrasonic transmitters (internal tags) were inserted into small (34-38 cm TL) and large (58-81 cm TL) individuals. The tagged cod were also divided into two groups, those released at the capture site ('replanted') and those released distances of 15, 25, and 55 km ('transplanted') from their capture location (Table 4.1). The size of fish tagged and the transplant distances were based on previous research. Morris et al. (2007) found that Gilbert Bay cod from 33-34 cm TL were not migratory, and occupied a small home range. Observed changes in length-frequency distributions between May and August (Morris and Green 2002) suggested that Gilbert Bay cod begin to migrate when between 35 and 40 cm TL. Information from commercial tag returns in areas outside the MPA indicated that larger commercial sized fish (> 45 cm TL) moved away from zone 1a to areas including those outside the MPA.

Fish were tagged internally with Vemco model V13 and V16 ultrasonic transmitters (www.vemco.com) with dimensions of 13 x 36 mm and16 x 68 mm respectively, having

transmit intervals between 1.5 to 5 minutes and the same power output (158 dB re 1μPa @ 1m). The tag weight in air was less than 1 % of the body mass of the fish. All tags were tested before insertion into the body cavity.

### 4.3.3 Data collection

Beginning in 2005, a network of Vemco ultrasonic receivers (models VR2 or VR2W ) was established to detect and track individuals having ultrasonic transmitters, year round (Figure 4.1). The receiver network developed over a several year period, building from 10 receivers in 2005-2006, 20 receivers in 2008, and 35 receivers since 2009 which largely covers the entire range of the population. The completed detection array covered approximately 330 $km^2$. One receiver was located at each station except for MPA zone 1a (Figure 4.1) which had six receivers. Movement outside zone 1a distinguished between resident individuals and those that moved seasonally. Receiver stations were positioned to detect fish movement throughout the study area (Figure 4.1), often in narrow passages and near headlands around which fish would have to pass while moving from one inlet to another. Receivers were also placed away from areas of fishing activities such as scallop dragging which damaged and removed moorings during this and earlier studies in the area (Morris et al 2001b).

Receivers were deployed in depths ranging from 10 to 150 meters with an attached buoyed line to suspend the receiver several meters above the sea floor. A 10-kg weight, connected to a ground-line stretched along the bottom, anchored the buoyed line to the

seafloor. Ground lines (18 mm polysteel rope) were held in place by a 10 kg chain on each end and 1- 4 equally spaced concrete cinder blocks (13 kg) along its length. The end-positions of each ground line was recorded using a Garmin model 60CSx hand held GPS. In order to retrieve the receivers a "creeper", a specialized grappling hook designed to catch rope, was dragged between the ground line end-positions, a procedure known as "creeping". Receivers were brought to the surface to replace batteries and/or retrieve transmitter data.

Various small boats (4 - 12 m) were used to set and retrieve receivers. Receiver positions were recorded using a GPS in order to improve retrieval success. Receiver retrieval success was high during calm conditions compared to poor weather conditions with large swell, high winds and tide. In shallow depths (<15 m) the receivers were retrieved by hand using a smaller boat, whereas deeper sites required larger boats equipped with a hydraulic hauler. In both cases, a boat speed of approximately 2-4 $km \cdot hr^{-1}$ proved most effective for creeping. As depths increased, particularly at depths greater than 100 m, additional rope was deployed to increase the scope of the creeping line from approximately 2:1 to 3:1 (rope: depth) and added additional weight (a 10-kg chain 30-40 meters in front of the creeper) to help maintain creeper contact with the bottom, particularly during periods of large swells.

### 4.3.4 Data analysis

Data from receivers were incorporated into an Oracle relational database that contained tagging data, receiver data and deployment-retrieval history. To remove the likelihood of false detections from the receiver data, tag detections were considered valid only when at

least two detections were received from a tag within a 30 minute period on a given receiver. A fish was then considered to have been within 1 km of that receiver. Single tag detections were only included in the analysis when multiple detections from the same tag were recorded on two adjacent receivers before and after a single detection.

One hundred and nineteen Atlantic cod were tracked between 2005 and 2011 (Table 4.1). Of the 72 fish caught and "replanted" at the capture location, 59 were large (58-81 cm TL) and 13 were small (34-38 cm TL). Large fish transplanted in 2006 and 2009 (n=19) within Gilbert Bay were included with replanted data analysis once fish were at large for one year because they returned rapidly to their release site and resumed behavior typical of replanted fish for the remainder of the observation period. The 47 fish "transplanted" 15, 25 or 55 kilometers from their original capture site within zone 1a (Figure 4.1) included 30 large and 17 small individuals. Fish that moved away from zone 1a and did not return to overwinter were classified as strays, whereas those that moved out of zone 1a and returned during the same year were considered migratory.

## 4.4 RESULTS

Recapture of externally tagged cod provided data on site fidelity of fish within the zone 1a core area. Although zone 1a is an overwintering area for large fish, it is also an important area for early life history stages; many juvenile and adults fish resided there year round. From 1998 to 2009, 314 of 8213 cod were recaptured during spring and summer research sampling, of which 274 tags had legible information upon recapture.

Recaptures during research sampling in zone 1a indicate very site specific fish. Most fish were recaptured less than 500 meters from their initial tagging location, up to 9 years at large, both during the spawning season and during summer (Figures 4.2, 4.3, 4.4). Because most sampling sites were greater than 500 m apart, most fish listed as recaptured within 500 meters of the initial capture site were recaptured at their initial tagging site. The high degree of site fidelity of tagged fish sampled in zone 1a is biased in that our sampling was restricted to this area. Sampling the entire home range was simply not feasible during the limited sampling period available, and low catch rates outside zone 1a further complicated broader spatial sampling. Therefore, predictions of homing behaviour and limited dispersal over time were tested primarily through acoustic telemetry studies.

### 4.4.1 Movement of Gilbert Bay cod

The annual movement of large cod tagged with an internal transmitter out of zone 1a occurred during late May and June. Fish returned to zone 1a over a longer time period, between July and November (Figure 4.5). The annual timing of fish movement out of zone 1a typically occurred after the spring sampling period, with the exception of 2006. Fish began to move out of zone 1a substantially earlier in 2006 than in other years. All ultrasonically tagged fish had moved out of zone 1a during 2006 before any ultrasonically tagged fish moved out of this zone in all subsequent years. Completion date of the spring freshwater runoff period occurred earlier in 2006 than any other subsequent year which could contribute to the timing of the spring outmigration (Figure 4.6).

Large and small fish that moved away from zone 1a during 2009-2011 did not move beyond 40 km from zone 1a (Figure 4.7), indicating a population home range of less than 330 $km^2$ (the maximum area of Gilbert Bay within 40 km of zone 1a). Most fish that moved beyond the boundary of the MPA nonetheless remained within 10 km, with only 9 fish detected by the most distant hydrophones to the north and south. Small cod (34 – 38cm TL) remained residents of the MPA during the first year after tagging but more small fish were likely to migrate during the second and third year of tracking. These small cod moved as far as large cod. The amount of time migratory fish (large and small) spent away from zone 1a varied, but never exceeded four months (Figure 4.8). Movement away from zone 1a during 2009-2011 was directional in that cod moved toward zone 3 rather than zone 1b. Beyond zone 3, Gilbert Bay cod had the opportunity to disperse, into more open coastal areas and Alexis Bay (Figure 4.9).

Although small fish were more likely to stray, high rates of homing to the same overwintering and spawning location were observed for both large (93%) and small (70%) fish over several years. Most small fish did not move outside zone 1a during the first year of tagging (10 of 13 individuals) but several (11 individuals) did migrate in subsequent years of the three-year period. Those small fish that moved outside zone 1a were significantly more likely to stray than large fish ($P=0.017$, Fisher exact test, Table 4.2). Interestingly, some stray fish (three large and one small) spent the winter in the main arm of Gilbert Bay, but moved back into zone 1a, a well known spawning area (Chapter 3), during the spawning period (May – June) before they returned to the Main Arm of Gilbert Bay.

Small fish were less migratory than large fish (Table 4.3). Comparison of the movements of large and small fish that included 2009 data or pooled data from 2005-2009 and 2011 both showed consistent and statistically significant differences in their movement patterns (Table 4.3). The behaviour of small and large fish transplanted 15 and 25 km also differed significantly. Large transplanted fish returned to the capture site and small fish did not (Fisher's exact P=0.007) (see section 4.4.2).

Ultrasonic tags used in this study lasted for several seasons and provided data for three years. Twenty-one large cod and 9 small cod were tracked for approximately 900 days each, until their tags expired. The small cod (35 cm TL SD 1.5 cm, n=9) became increasingly more likely to move away ("migrate") from zone 1a during each subsequent year they were monitored. Once a small cod moved away from the tagging area it continued to seasonally migrate in subsequent years (Figure 4.10). Although most large cod moved away from zone 1a during the first year of tagging, they became increasingly less likely to move in subsequent years (Figure 4.10). After a large cod did not move from zone 1a during a given year, it remained there in subsequent years. One small fish did not migrate during the third tracking year, after migrating during the previous two years.

### 4.4.2 Transplanted fish

The movement pattern of transplanted fish provided observed data, which was compared to the movement pattern of replanted fish that provided expected movement patterns of

both large and small fish in the population. Based on movement of replanted individuals, the transplant distance of 15 km was expected to be within the home range of large fish but outside the home range of small fish. On the one hand, 70% of small transplants were not expected to return to the capture or "home site" after transplanting because the replant data (observed data) showed that 70% of small fish were not migratory. Therefore the working hypothesis predicted that small transplanted fish would lack the experience necessary to return. On the other hand, 78% of large transplanted fish were expected to return to the home site (see Table 4.3). An exact binomial test of goodness-of-fit confirmed predictions based on data from a balanced design in 2009 and also from pooled data from different years (Table 4.3). Small fish showed no significant difference between expected and observed movement patterns (P=0.3 and P=.054 for balanced and pooled data respectively, see Table 4.3) as did large fish (P=1.0 and P=0.13 for balanced and pooled data respectively).

A higher, but not significantly different (P=0.12 Fisher Exact) proportion of large transplants returned (100%) than expected (78%). Most (11 of 17) returned within a 2-week period before the end of the spawning season, and then resumed a seasonal migration pattern typical of large replanted fish.

Small cod did not return to the home site directly after transplant, and most never returned during the 900 days over which they were tracked (Figure 4.11). Only two individuals returned in their first year, another in its second year and a fourth small cod returned to the home site for the first time three years after tagging. Thirteen other small

transplanted fish did not return during the 900 day life expectancy of ultrasonic tags. Some of these fish were detected while moving increasing distances away from the home site until they were last detected by the most distant seaward hydrophones in our detection array. Of the four small fish that returned to their release site, three of them were among the largest of this group (34-38 cm TL), and could have been one or two years older than the smallest fish in this group (Chapter 2).

Assuming that small cod did not return to the home site because they lacked experience outside the home range, it was also expected that large fish would not return to a home site when transplanted a similar distance (15 km) beyond their home range. In June 2011, 11 large cod were transplanted from the capture location in zone 1a during the spawning season to a release site 55 km away, a distance that exceeded the expected home range of large Gilbert Bay cod by at least 15 km, based on the movements of large replanted fish. Fish were released in St. Michael's Bay near the community of Pinsent's Arm (Figure 4.1). After the initial release at the St. Michael's Bay site, several fish returned repeatedly to the release site sometimes weeks apart, but not the home site. One of the transplanted fish was captured in a commercial whelk pot on July 18$^{th}$, approximately 2 km from the release site, and was returned by the harvester to Fisheries and Oceans Canada. Between June and October, hydrophones detected two other fish along the northern periphery of the Gilbert Bay array, but those individuals did not return to zone 1a. Interestingly, the one fish that returned to zone 1a followed a non-direct route into an area that many Gilbert Bay cod are presumably familiar with. After by-passing the northern entrance to Gilbert Bay as it moved south along the coast, it entered the mouth of Alexis Bay where

some replanted cod were detected. It then moved northward into Gilbert Bay back to zone 1a, and arrived at the capture site on August 17th, 2011. Only one of 11 large cod transplanted to St. Michaels Bay returned to the capture site within 12 months after transplant, suggesting that Gilbert Bay cod transplanted outside their home range are unlikely to return to the home site.

### 4.4.3 Mortality

Sources of potential mortality among our experimental fish include tagging, natural causes, and fishing. In our study tagging mortality was < 1% (1 of 119 individuals). This low mortality was attributed to the fact that fish were caught in shallow depths, mostly during cold conditions, tagged, and released quickly by experienced personnel. During summer 2008, a group of 4 fish died as a result of warm water conditions during a long-distance (40 km) transplant. These fish were detected for less than one day after release, and mortality was assumed because of the short detection period. It is possible that these fish moved quickly away from the receiver array never to be detected again but it is unlikely given that all other fish in this study were detected for much longer time periods and often on multiple receivers. Unexpected tag disappearances from within the array, long before the tag expiration date but after a period of regular detections, provides an estimate of mortality.

Disappearances of ultrasonically tagged cod from within the study area were low, indicating low mortality from natural causes and fishing combined, during the 2009-2011 monitoring period. One of 13 (8%) small, replanted fish disappeared from within the

detection array during the entire 3 year period (~900 days). For large fish, 2 of 22 (9%) in 2008, 6 of 40 (15%) in 2009, and 2 of 20 (15 %) in 2010 disappeared from within the detection array area. Fish detections that disappeared from the detection array during a third year post tagging were not considered potential mortalities because tag batteries likely expired. Detections from only one fish disappeared while in zone 1a, which occurred in March 2010. Within 30 days, detections disappeared from two other tags located in the Main Arm of Gilbert Bay.

## 4.5 DISCUSSION

### 4.5.1 Timing of Migration

Ultrasonically tagged cod, both small and larger adults, from the unique Gilbert Bay population moved within a distance of 40 km from the zone 1a location where they were initially tagged during the spawning season. Almost all individuals returned to the same specific location during late summer and fall and overwintered there, while some individuals spent an entire year or more within zone 1a. This small region provides a core area for much of the existing population. Fish within zone 1a, were mostly recaptured less than 500 meters from the initial capture location, and were typically recaptured within an area of 2 hectares during spring and summer sampling. Although sampling was concentrated in zone 1a, telemetry data indicated strong homing and site fidelity among large and small fish to this core area. This finding emphasizes the importance of protecting fish in this specific area; otherwise, fish are highly vulnerable to overfishing. Timing of the outmigration began near the end of the spring freshet each year (Chapter

2), after the spawning period as water temperatures increased but before the early July arrival of capelin (Figure 4.12). The end of the spring freshet occurred earlier in 2006 than other years and tagged cod also moved out earlier that year, suggesting that the spring freshet, at least in part, is somehow related to out-migration.

Large Atlantic cod can migrate distances of many hundreds of kilometres and it is widely assumed that most individual cod spawn each year and then undertake a feeding migration (Taggart 1997; Templeman 1974; Bergstad et al. 1987). In this study, most large fish moved away from the spawning area during the first year tagged, but were only half as likely to migrate to coastal areas in consecutive years. This observation could represent a sampling bias towards active fish, since fish were sampled by angling during the spring spawning period and potentially favouring individuals most likely to migrate that year. It is unlikely that tagging itself increased the likelihood of migration because large cod tagged during summer (Morris and Green unpublished data, one cod in this study) and most small cod tagged in spring did not migrate after tagging.

### 4.5.2 Locally adapted spawning and migration behaviour

Cod typically feed less during spawning (Fordham and Trippel 1999; Skjaeraasen et al. 2004), and therefore likely increase foraging activity after the spawning season. In Gilbert Bay, the timing and location of spawning occurred early in the ice free season over a short time period that correlated with the timing of the spring freshet (Chapter 3). A short distance and short duration seasonal feeding migration occurred after spawning (Chapter 5) when water temperatures were within the preferred temperature range of cod

(4-10 °C, from late June until November) (Righton et al. 2010; Chapter 2). The low energetic cost associated with a short migration distance and duration could reduce mortality (Finstad and Hein 2012). There are local adaptive advantages for Gilbert Bay cod to spawn at a time and place that retains eggs and larvae and over a short time period that enables the longest foraging period possible during a relatively short growing season (Chapter 3). Together, these behavioural characteristics likely enhance growth and reproductive success in the Gilbert Bay environment, and provide indirect evidence of locally adaptive behaviour.

### 4.5.3 Experience (habitat selection versus home site-familiarity)

The failure of Gilbert Bay cod (both small and large) to return to their home site after transplant 15 km outside their known home range is consistent with the hypothesis that homing requires migratory experience. Nonetheless, in the absence of data of small and large fish with and without experience, this inference remains somewhat speculative but consistent with the mechanism proposed by the adopted migrant hypothesis (McQuinn 1997). Small fish that remain within a small area lack such experience and large fish with migratory experience within a relatively small area (within 40 km of zone 1a), did not return when transplanted just 15 km outside their estimated home range. It is unlikely that differences in sensory capabilities, including olfaction, between large and small fish are the reason larger fish can return from a 15-km transplant distance whereas small fish can not. Only 3 of 14 small transplanted fish returned to the release site and they remained there for the duration of that summer and through the following winter, whereas the other small transplanted fish continued to move over a larger area. Some small replanted fish

that moved more than 15 km away from their home site returned successfully. The pattern observed in Gilbert Bay cod suggests they can home to a known site based on a single experience with new areas. The pattern is also consistent with learned piloting, during which fish can move across familiar areas by referring to learned land marks (either through exploration or following others) (Dodson 1988; Kieffer and Colgan 1992). When large cod were transplanted 55 km from the capture site (15 km outside the known home range) their behavior appeared similar to small cod transplanted 15 km from their home site; most did not return to the home site and did not remain at the transplant site. Preliminary data from 2012 indicated that none of the large transplanted cod returned to the release site in St. Michael's Bay between October 2011 and June of 2012, and no additional fish had returned to the home site by September 2012. Whether Atlantic cod in other populations rely on experience to conduct long distance migrations remains unknown, but other authors (Rose 1993; Windle and Rose 2005) have speculated that some do. Furthermore, learning is described as an important part of natal homing and the formation of locally adapted populations in other species such as salmon (Hansen and Jonsson 1994).

This study found that most small transplanted fish continued to move, often over increasingly large distances after being moved out of their home range. Several fish moved outside the population's home range and beyond our detection area. Cote et al. (2004) suggested that site-specific behaviours observed in juvenile cod reflected habitat preferences that reduced predation risk. In the current study, however, small fish transplanted outside their home range did not remain near the release site and moved

greater distances than the replanted fish. Small transplants did not appear to reside in areas between two hydrophones or within the detection range of a single hydrophone for a long period of time. Two small fish that did return to the home site remained at the home site, overwintered, and then migrated to the coast the following spring, a pattern among large replanted individuals.

Large cod exhibited site-specific homing behaviour. Most large fish transplanted within their home range rapidly returned to the home site over distances of 15-25 kilometers. Those large fish that did not return within several days, returned later in the season during the typical return migration period expected for replanted fish. However, most large fish transplanted to areas outside the home range (55 km) did not return. This pattern suggests a critical role for experience, and possibly the use of learned cues, in Gilbert Bay cod homing.

The inference that these fish would return to a specific home site if they had the ability to do so can be implied, based on observed homing behaviour of other individuals and the importance of homing described in previous studies (e.g. Rose, 1993). Previous work also emphasizes the importance of natal homing in Atlantic cod for maintaining separate populations (Svedang et al. 2007). For coastal cod populations in Norway, Olsen et al. (2008) suggested that life history divergence is maintained on a scale of tens of kilometers in coastal cod. Local population ranges calculated from microsatellite DNA divergence patterns, capture-recapture data and site fidelity research suggest similar small-scale population structure (Knutsen et al. 2003; Jorde et al. 2007; Espeland et al.

2006). However, individuals from different populations could occupy the same habitats as a result of seasonal movement patterns. Therefore, it was concluded that fish not returning within several months and up to a year after transplant were unable to navigate back to the home site. Individuals that lack experience with a migratory route are unlikely to return.

Whether fish use social learning to aid in navigation during large–scale migrations remains an open question (Odling-Smee and Braithwaite 2003); however, Rose (1993) suggested learning is important in bank-scale feeding migrations and other complex behaviours in Atlantic cod. Atlantic cod form large aggregations during spawning and migration (Rose 1993), exhibit mate competition and choice (Hutchings et al. 1999; Rowe et al. 2007), and exhibit complex vocalizations (Brawn 1961; Rowe et al. 2004; Rowe and Hutchings 2006). It has been suggested that younger individuals may learn migration routes from older individuals while shoaling (Rose 1993). Atlantic cod in Placentia Bay that were tagged and transplanted during spawning were more likely to return to the same ground if they were released along a known migration route compared to those released in potentially unfamiliar areas of the bay (Windle and Rose 2005). From a fisheries perspective, the role of learning has been raised with respect to population recoveries (ICES 2007; Petitgas et al. 2006), however, demonstrating an effect of loss of experienced fish on population recovery has proven difficult with little direct evidence available.

Since the northern cod population collapsed two decades ago, high total mortality rates (Z) have continued such that few northern cod > 6 years old were observed in the offshore for many years (DFO 2011 CSAS). Atlantic cod throughout their range typically become sexually mature at 4-6 yrs, and require more energy for reproduction, which could influence migratory behaviour (Olsen et al. 2004; 2005) and/or mortality rates. Studies assume that the instantaneous rate of natural mortality (M) for northwest Atlantic cod was 0.2 per year historically (Hutchings et al. 1999) but assessments of survey data suggest even higher values of M for offshore Atlantic cod stocks in the Newfoundland and Labrador region during portions of the (1998-2012) time period of our study (DFO 2011 CSAS). High offshore total mortality (Lilly et al 2006) contrasts with lower inshore mortality including our study and for Atlantic cod tagged in Smith Sound (Brattey et al 2008). In Smith Sound, Brattey et al. (2008) observed high rates of homing to a specific area to overwinter and very low total mortality rates, <14% Z (combined fishing and natural mortality) per year. Differences in mortality between inshore and offshore areas may explain the persistence of older cod (i.e. > 6 yrs) among inshore Atlantic cod populations in the Newfoundland and Labrador region while the abundance of older age classes in offshore populations remained low during much of the post-moratorium period.

The expulsion of tags implanted into the body cavity of fish has been reported to be common among some fish species, e.g. catfish, (Jepsen et al. 2002), but does not appear to be common among the Atlantic cod in this study. The long term tracking periods and low number of tag dissapearances in this study suggests that tag expulsion is low. A small number (three) of cod dissapeared for unkown reasons from within the detection array

and it is possible that the tag was expelled, but the fish could have died from natural mortality or if the tag malfunctioned. It is perhaps unlikely that these three fish were caught because they disapeared during winter, when the area was covered with ice and cod fishing at this time of year is unlikely. However, all other disappearances of ultrasonically tagged cod occurred outside the spawning grounds during the fall and early winter, when fishing mortality is more likely. During the study, two tags were caught in commercial fishing activities and returned; however, unreported tag recaptures are common in this area (Morris 2003).

## 4.6 CONCLUSIONS

Homing and site-specific behaviour observed in this study, and other accounts of extreme site-specific behaviour for cod populations elsewhere (Skjaeraasen et al. 2011 and references therein) indicates the importance of home sites. External and ultrasonic tagging experiments in this study demonstrated strong site fidelity and homing behavior in small and large Gilbert Bay cod. Transplant experiments of ultrasonically tagged cod examined the role that experience may play in the migration and navigation ability of Gilbert Bay cod. These experiments indicated that experience plays an important role in the ability of Gilbert Bay cod to return to their core areas after migrations to the coast. Specific habitat did not appear to affect the behaviour of large or small cod, in that individuals moved through a wide range of potential habitats. These findings are similar to those of discrete populations of Atlantic cod located in close proximity (30 km) to each other in Norway which display site-specific behaviour even where suitable habitat is available over larger spatial areas (Knutsen et al. 2003; Jorde et al. 2007).

Movement patterns of immature and adult Atlantic cod in Gilbert Bay helps to maintain the local population through strong homing and site-specific spawning behavior. Primarily sedentary small fish become migratory at approximately 35-40 cm TL, corresponding to a size typical for sexual maturation in this species. This change in behaviour may be driven by increased energetic requirements for reproduction. The migratory behaviour of Gilbert Bay cod relates to feeding opportunities along coastal areas, which the following chapter addresses.

Table 4.1. Summary of ultrasonic tagging information for replanted and transplanted Gilbert Bay cod. Small cod ranged in size from 34-38 cm TL and large cod were 58-81 cm TL.

| Experimental group | Size category | Tag season | Year | Mean TL (SD) | Transplant distance (km) | Sample size |
|---|---|---|---|---|---|---|
| Replants | Large | Fall | 2005 | 64.8 (3.9) | 0 | 10 |
| | | Spring | 2006 | 64.0 (11.3) | | 2 |
| | | Spring | 2008 | 65.9 (4.8) | | 22 |
| | | Summer | 2008 | 76 (na) | | 1 |
| | | Spring | 2009 | 60.1 (4.3) | | 10 |
| | | Spring | 2011 | 57.5 (7.0) | | 14 |
| | Small | Summer | 2007 | 34.7 (3.1) | | 3 |
| | | Spring | 2009 | 36.1 (1.5) | | 10 |
| Transplants | Large | Spring | 2006 | 69.5 (10.7) | 25 | 5 |
| | | Spring | 2006 | 61.3 (4.8) | 15 | 4 |
| | | Spring | 2009 | 62.0 (3.4) | 15 | 10 |
| | | Spring | 2011 | 57.2 (5.3) | 45 | 11 |
| | Small | Summer | 2007 | 34.6 (0.5) | 25 | 4 |
| | | Summer | 2007 | 34.7 (0.5) | 15 | 3 |
| | | Spring | 2009 | 36.6 (1.4) | 15 | 10 |

Table 4.2. Summary of straying for 11 replanted Gilbert Bay cod. Fish were considered to stray if they did not return seasonally to zone 1a. A Fisher exact test showed a significant difference in straying (P=0.017) between large and small fish. Some fish stayed away for one winter and returned the following year. Strays are indicated as the number of fish that strayed among the number of fish tagged during a particular tagging experiment. Fish that spent <1 winter away are fish that stayed in Gilbert Bay's Main Arm during winter but returned to zone 1a during the spawning season.

| Size Group | Strays | TL (cm) | Tag year | Stray year | Overwintering Location | Winters Away |
|---|---|---|---|---|---|---|
| Small cod | 2 of 5 | 38 | 2009 | 2009 | Gilbert Bay | 2 |
| | | 36 | 2009 | 2009 | Gilbert Bay | 2 |
| | 2 of 5 | 35 | 2009 | 2010 | Gilbert Bay | <1 |
| | | 34 | 2009 | 2010 | Gilbert Bay | 1 |
| | 1 of 3 | 38 | 2007 | 2009 | Gilbert Bay | <1 |
| | | | | | | |
| Large cod | 3 of 50 | 72 | 2006 | 2006 | Gilbert Bay | <1 |
| | | 62 | 2009 | 2009 | Gilbert Bay | 1 |
| | | 57 | 2009 | 2009 | Gilbert Bay | 2 |
| | 3 of 36 | 62 | 2008 | 2009 | Alexis Bay | 2 |
| | | 64 | 2008 | 2009 | Gilbert Bay | 1 |
| | | 65 | 2008 | 2009 | Alexis Bay | 2 |

Table 4.3. Observed and expected behaviour patterns of large and small fish. The expected proportion of small and large fish to have migratory experience, and thus homing ability upon transport, was based on replanted fish behaviour. Observed data based on transplanted fish was similar to expected data. Balanced experimental design data from 2009 are presented separately. Data from other years are pooled (as indicated). A significant difference was found between large and small replanted fish (Fisher's exact $p=0.0011$) and those that were transplanted (Fisher's exact $P<0.001$). Replanted fish tagged in 2008 (n=22) were not included; 21 of 22 moved outside zone 1a but several did not move or were not detected as far as the transplant site (15 km).

| | | 2009 (Balanced design) | | 2005, 2006, 2007, 2009, (Pooled data) | | |
|---|---|---|---|---|---|---|
| Replanted fish (Expected) | | Resident | Migratory | Resident | Migratory | |
| | Small | 7 | 3 | 10 | 3 | 2007 (n=3), 2009 (n=10) |
| | Large | 1 | 9 | 4 | 18 | 2005 (n=10), 2006 (n=2), 2009 (n=10) |
| Transplanted fish (Observed) | | Did not return | Returned | Did not return | returned | |
| | Small | 8 | 2 | 14 | 3 | 2007 (n=7), 2009 (n=10) |
| | Large | 0 | 9 | 0 | 17 | 2006 (n=8), 2009 (n=9) |

Figure 4.1. Map of study area indicating MPA (Zones 1-3), Alexis Bay, and the coastal area where tagged cod were detected. Green dots indicate receiver stations. Zone 1a encompasses the spawning area. Most sampling was conducted in the area represented by 7 receivers closest to Shinneys River, zone 1a.

Figure 4.1

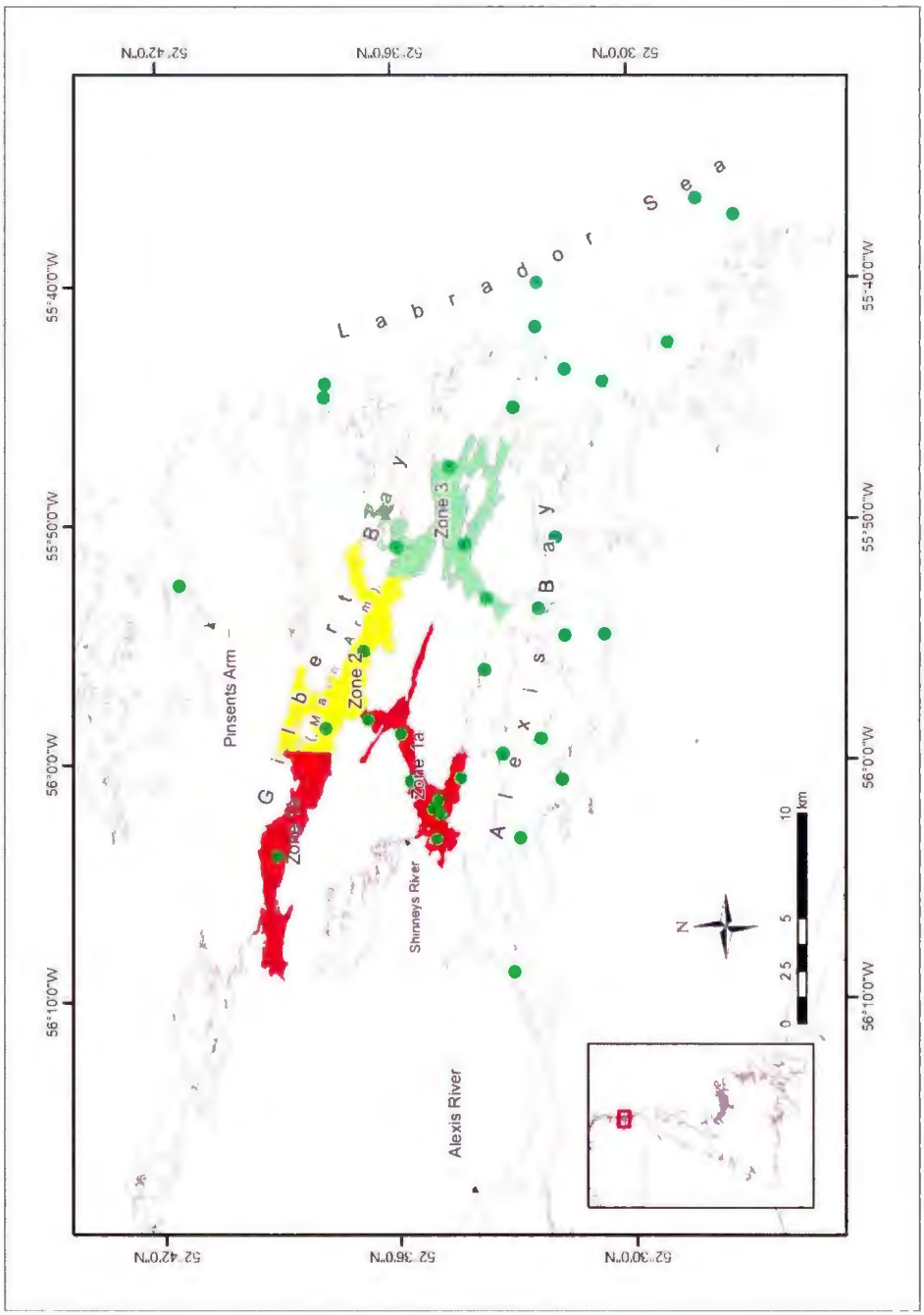

52°42'0"N
52°36'0"N
52°30'0"N
55°40'0"W
55°50'0"W
56°0'0"W
56°10'0"W
Labrador Sea
Gilbert Bay
Alexis Bay
Pinsents Arm
Zone 3
Zone 2
Zone 1a
Zone 1b
Shinneys River
Alexis River
N
0
2.5
5
10
km

Figure 4.2. Distance between mark and recapture locations for Gilbert Bay cod tagged externally during spring. Left panels include fish 40 cm or larger and right panels include fish smaller than 40 cm. Top panels include fish recaptured during spring and bottom panels include fish recaptured during summer. Fish recaptured within the same year are identified as 0 winter. Fewer small fish were recaptured because they grew into a larger size category while at liberty. Fewer fish were caught and tagged during summer.

Figure 4.2

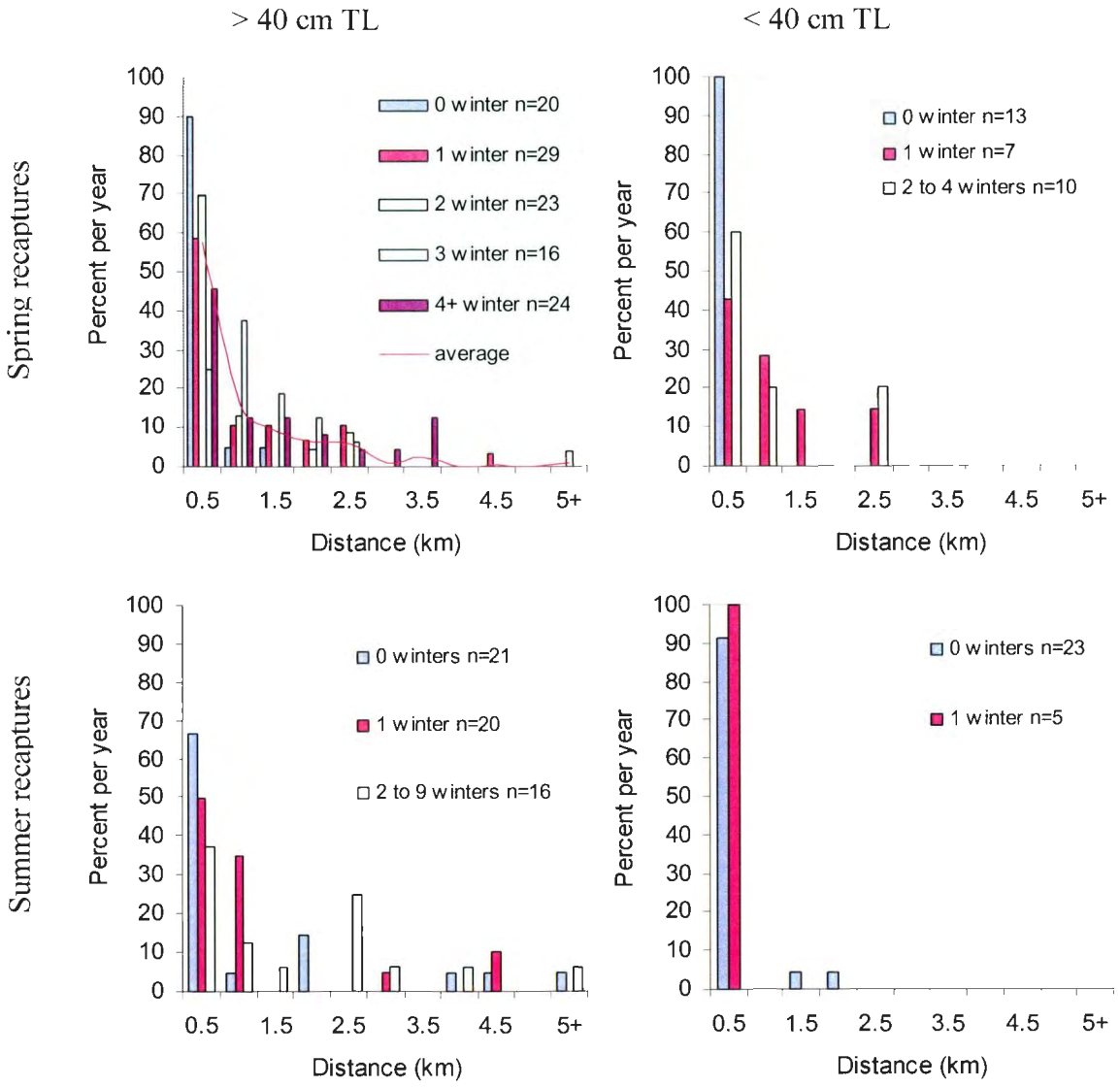

> 40 cm TL
< 40 cm TL
Spring recaptures
Summer recaptures
Percent per year
Distance (km)
0.5
1.5
2.5
3.5
4.5
5+
0 winter n=20
1 winter n=29
2 winter n=23
3 winter n=16
4+ winter n=24
average
0 winter n=13
1 winter n=7
2 to 4 winters n=10
0 winters n=21
1 winter n=20
2 to 9 winters n=16
0 winters n=23
1 winter n=5

Figure 4. 3. Distance between sites of mark and recapture for Gilbert Bay cod tagged during summer. Left panels include fish 40 cm or larger and right panels include fish smaller than 40 cm. Top panels show fish recaptured during spring and bottom panels show fish recaptured during summer. Fewer small fish were recaptured because they grew into the larger size category while at liberty. Fewer fish were caught and tagged during summer.

Figure 4.3

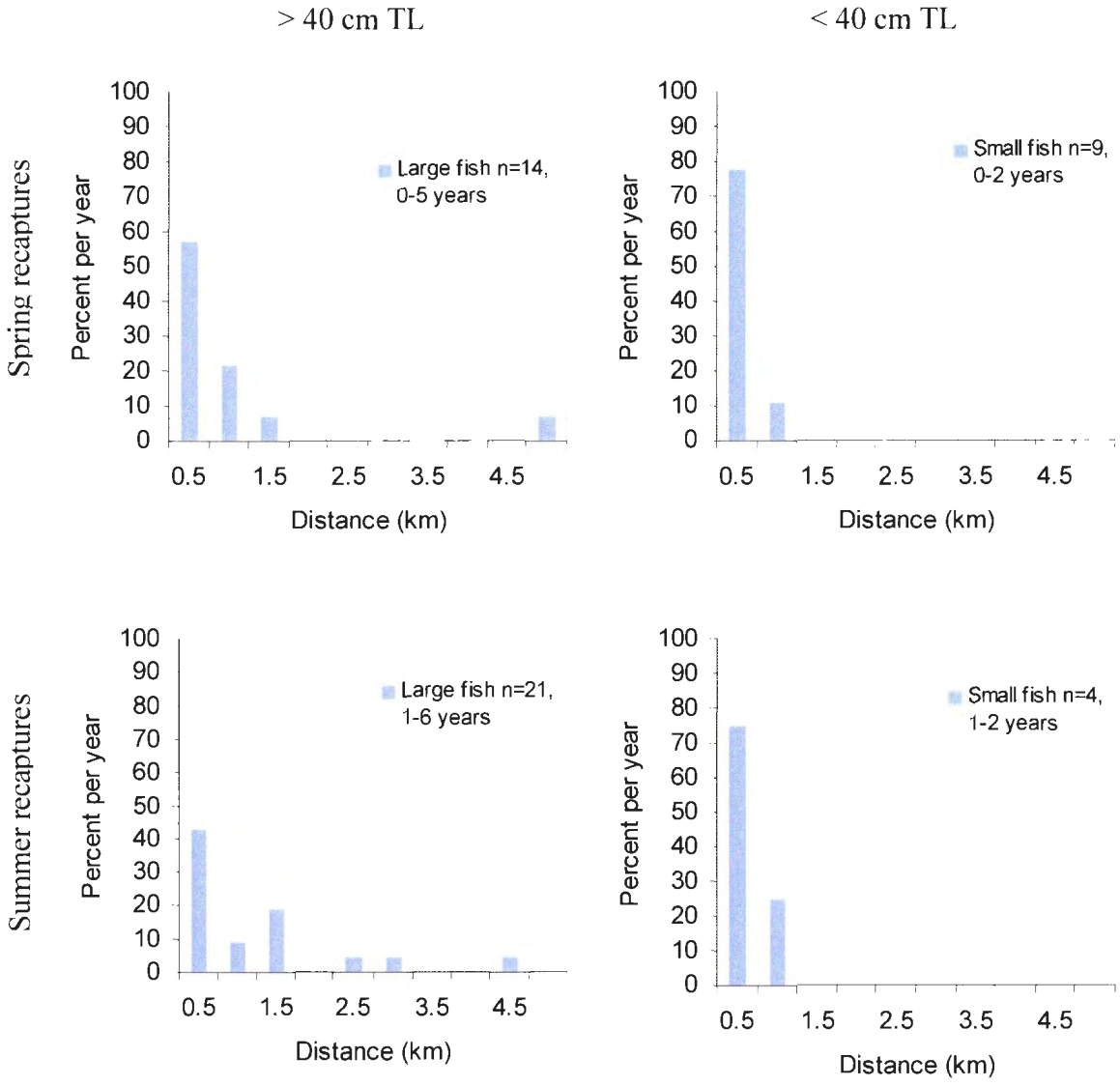

> 40 cm TL
< 40 cm TL
Spring recaptures
Summer recaptures
Percent per year
Distance (km)
Large fish n=14, 0-5 years
Small fish n=9, 0-2 years
Large fish n=21, 1-6 years
Small fish n=4, 1-2 years
0.5
1.5
2.5
3.5
4.5

Figure 4.4. Distribution of distances moved between initial capture and recapture during the 1998 to 2011 study period, for all 274 Gilbert Bay cod with legible data. The longest known period between mark and recapture where tag information was legible was 10 years.

Figure 4.4

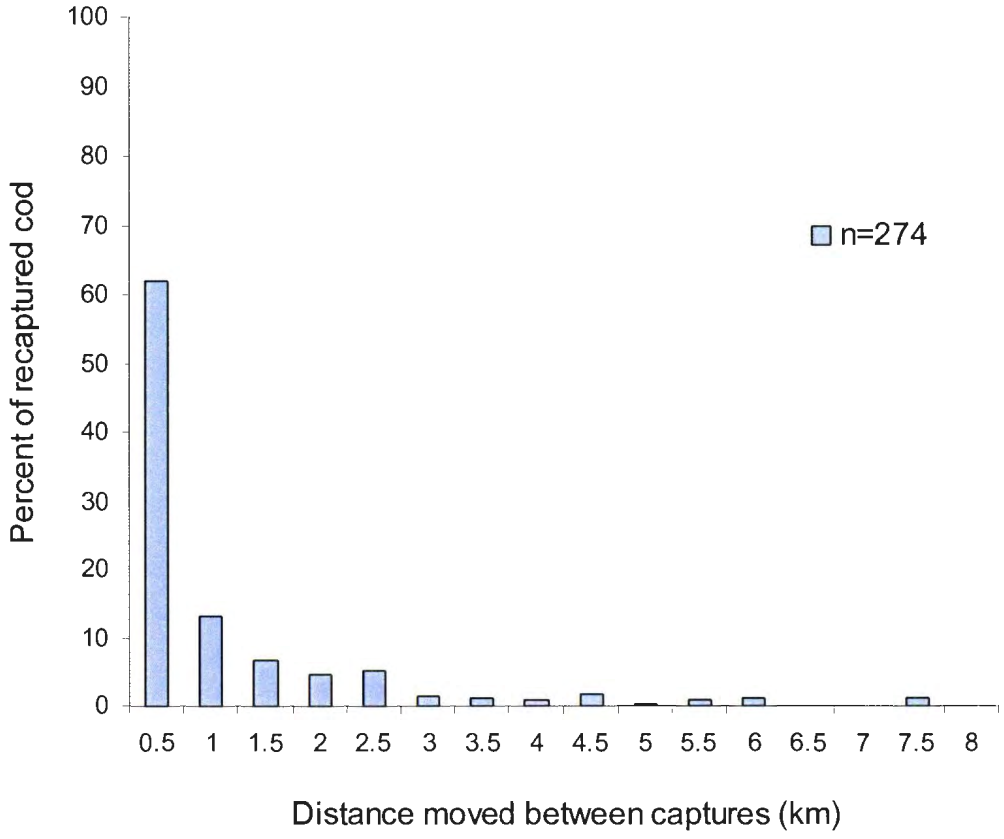

100
90
80
70
60
50
40
30
20
10
0
Percent of recaptured cod
n=274
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
Distance moved between captures (km)

Figure 4.5. Annual timing of spring migration from (blue) and back to (pink) zone 1a, based on telemetry of replanted fish with ultrasonic transmitters. Left panels shows data for the year fish were tagged, and right panels show data for the second year after fish were tagged. Two fish moved back into zone 1a before all fish had moved out in June, and another moved out after other fish started to return; these fish were considered outliers and are indicated by the three black squares (2007, 2008, and 2009). Data from 2011 are incomplete because 40% of cod had not returned to zone 1a at the time data were downloaded from receivers in October of that year. The lower right panel includes all data, including outliers.

Figure 4.5

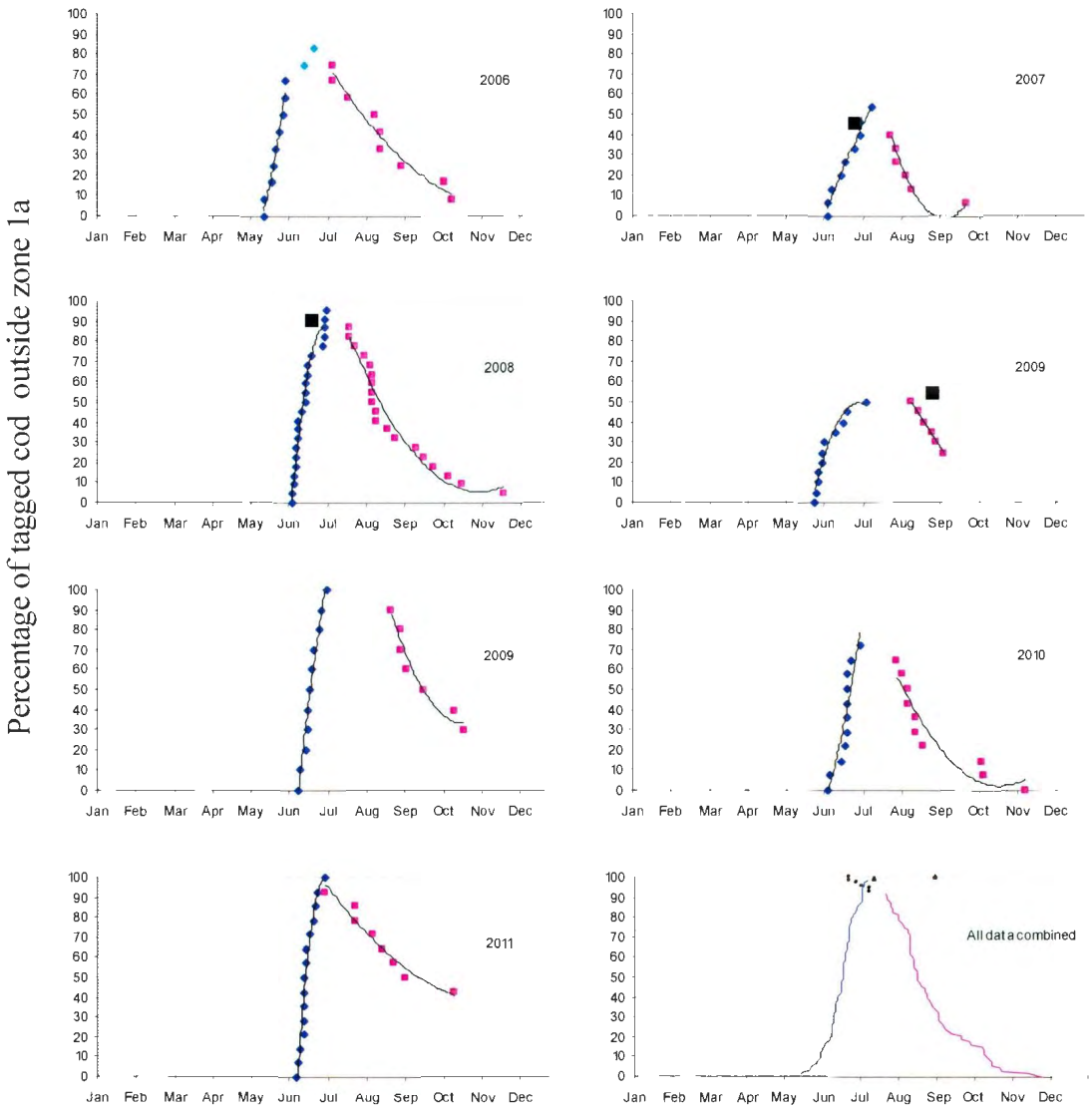

Percentage of tagged cod outside zone 1a
2006
2007
2008
2009
2009
2010
2011
All data combined
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

Figure 4.6. Annual flow data from the Alexis River indicating the timing of the spring freshet 2006-2010. The red line illustrates that in 2006, the spring runoff finished earlier than other years (Data for 2011 was not available at the time of writing).

Figure 4.6

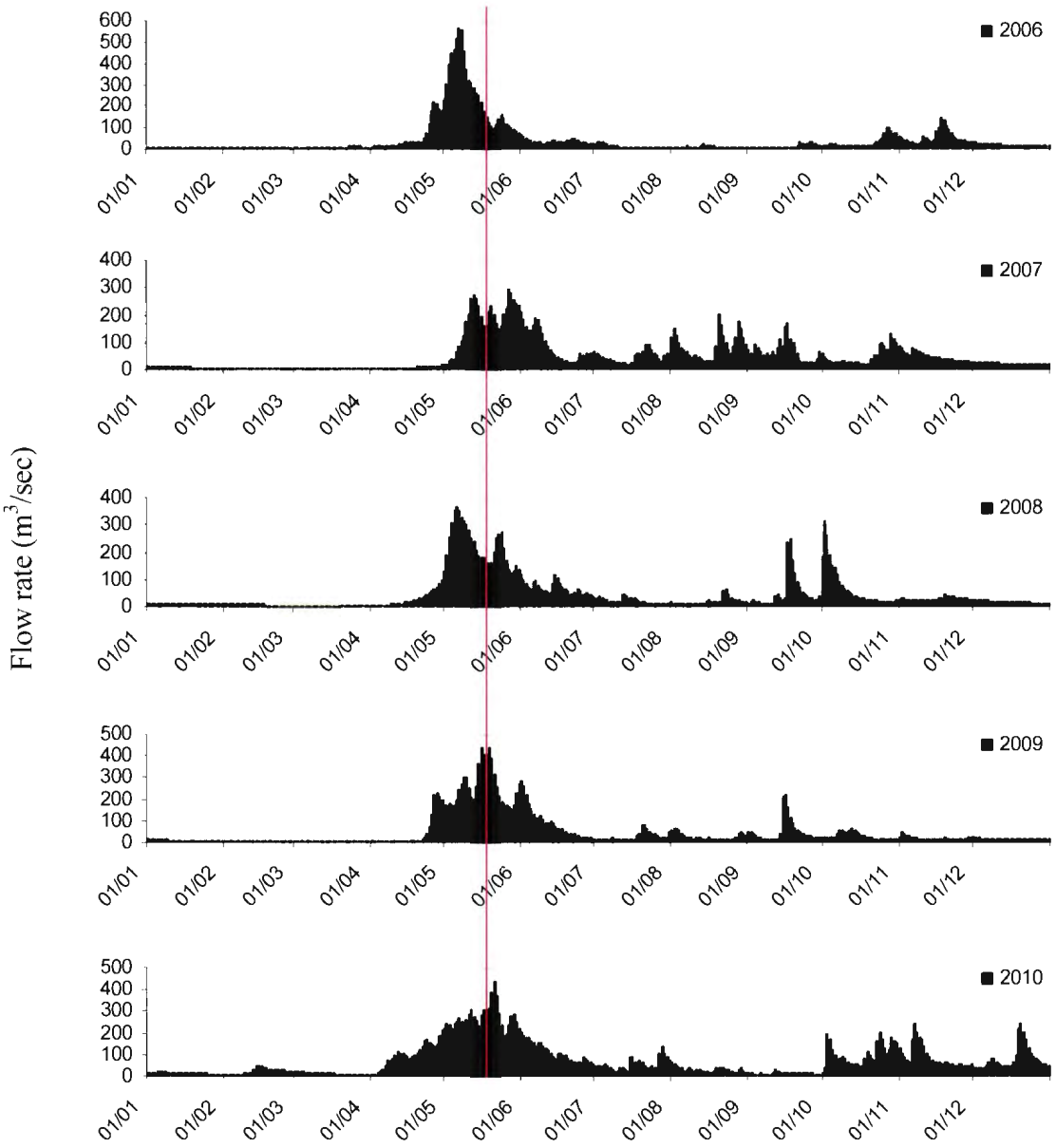

Flow rate ($m^3$/sec)
2006
2007
2008
2009
2010
01/01
01/02
01/03
01/04
01/05
01/06
01/07
01/08
01/09
01/10
01/11
01/12
Date

Figure 4.7. Maximum distance distributions of large (left) and small (right) ultrasonically tagged fish that were replanted, and subsequently moved out of zone 1a. Distance increases are shown in approximately 10 km distance intervals. The full array of receivers was not established until 2009, so earlier data were therefore not included.

Figure 4.7

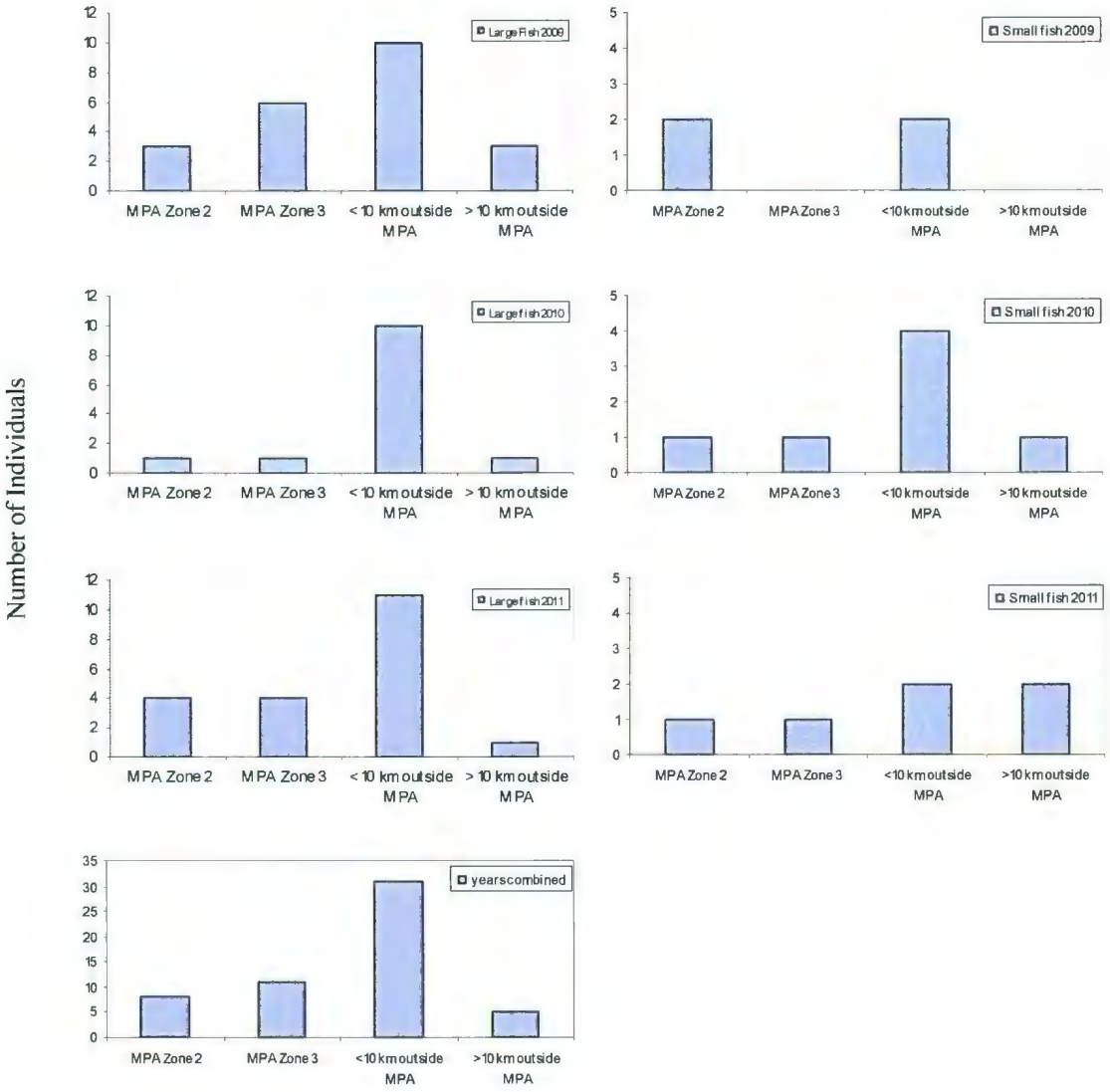
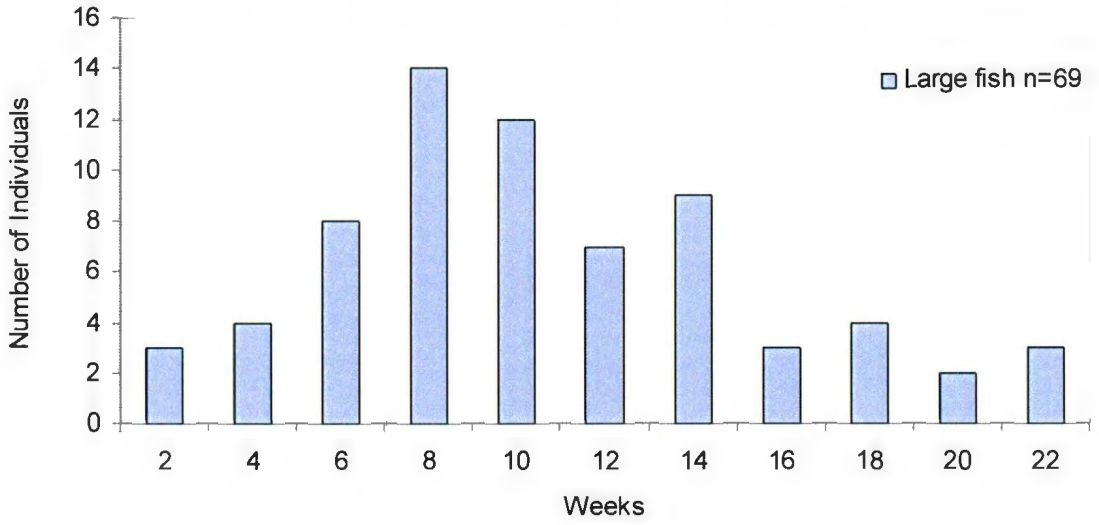

Number of Individuals
Large Fish 2009
Small fish 2009
Large fish 2010
Small fish 2010
Large fish 2011
Small fish 2011
years combined
MPA Zone 2
MPA Zone 3
< 10 km outside MPA
> 10 km outside MPA

Figure 4.8. Length of time that replanted ultrasonically tagged migratory fish spent away from zone 1a each year (2009-2011 combined) before returning that same year. Fish typically left zone 1a in June (see figure 2). The full array of receivers was not established until 2009, so earlier data were therefore not included.

Figure 4.8


Number of Individuals
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
18
20
22
Weeks
Large fish n=69

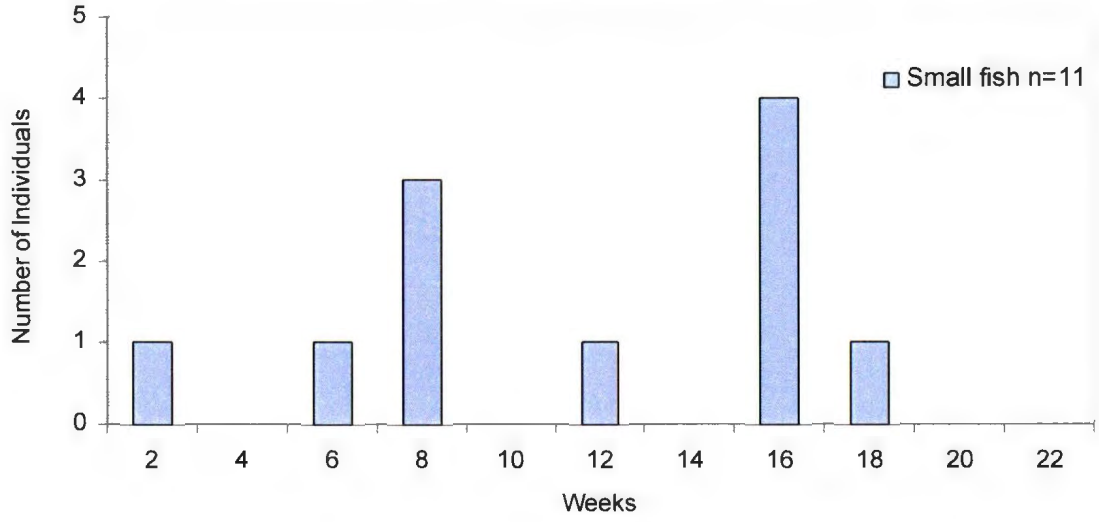

Number of Individuals
5
4
3
2
1
0
2
4
6
8
10
12
14
16
18
20
22
Weeks
Small fish n=11

Figure 4.9. Percentage of replanted ultrasonically tagged cod detected at each receiver station, indicating seasonal dispersal from the tagging site (zone 1a). Scale (100%) is represented by a black bar at each receiver station. The full array of receivers was not established until 2009, so earlier data were therefore not included.

Figure 4.9

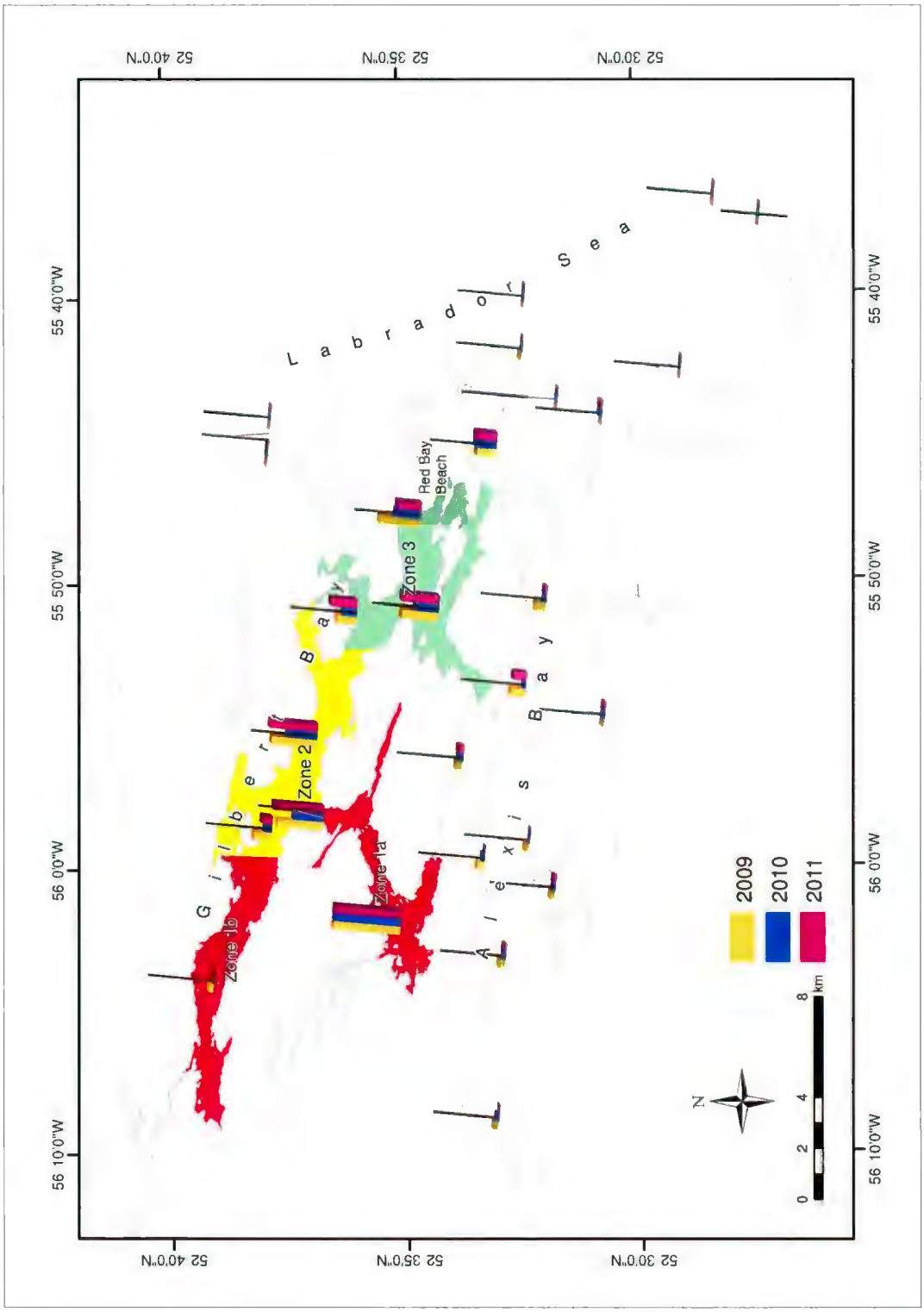

52 40'0"N
52 35'0"N
52 30'0"N
55 40'0"W
55 50'0"W
56 0'0"W
56 10'0"W
Labrador Sea
Red Bay
Beach
Zone 3
Zone 2
Zone 1a
Zone 1b
Gilbert Bay
Alexis Bay
2009
2010
2011
N
0
2
4
8
km

Figure 4.10. Migration patterns of small (n=9) and large (n=23) replanted Gilbert Bay cod, tracked over a 3-year period. Each column represents individual fish, where red represents non-migratory behaviour and blue represents migratory behaviour for each of three years during which an individual was tracked. Not all cod were tagged during the same year.

Figure 4.10

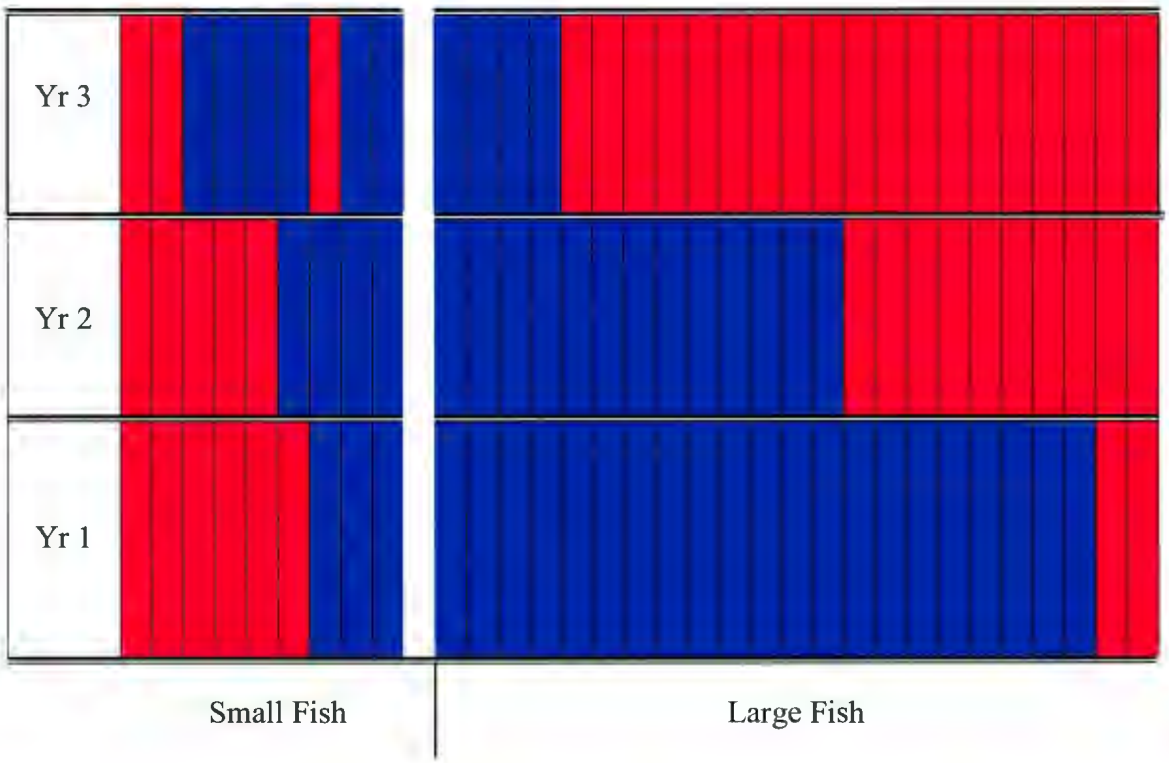


Figure 4.11. Return time (days) for small and large transplanted fish. Seventeen small (34-38 cm) and 17 large fish (57-81 cm) were transplanted distance of 15 and 25 km from zone 1a. Pink dots denote 13 small fish that never returned to zone 1a within the 900 day expected tag life. None of the five smallest fish (34 cm TL) returned, and only one of the 35 cm fish returned.

Figure 4.11

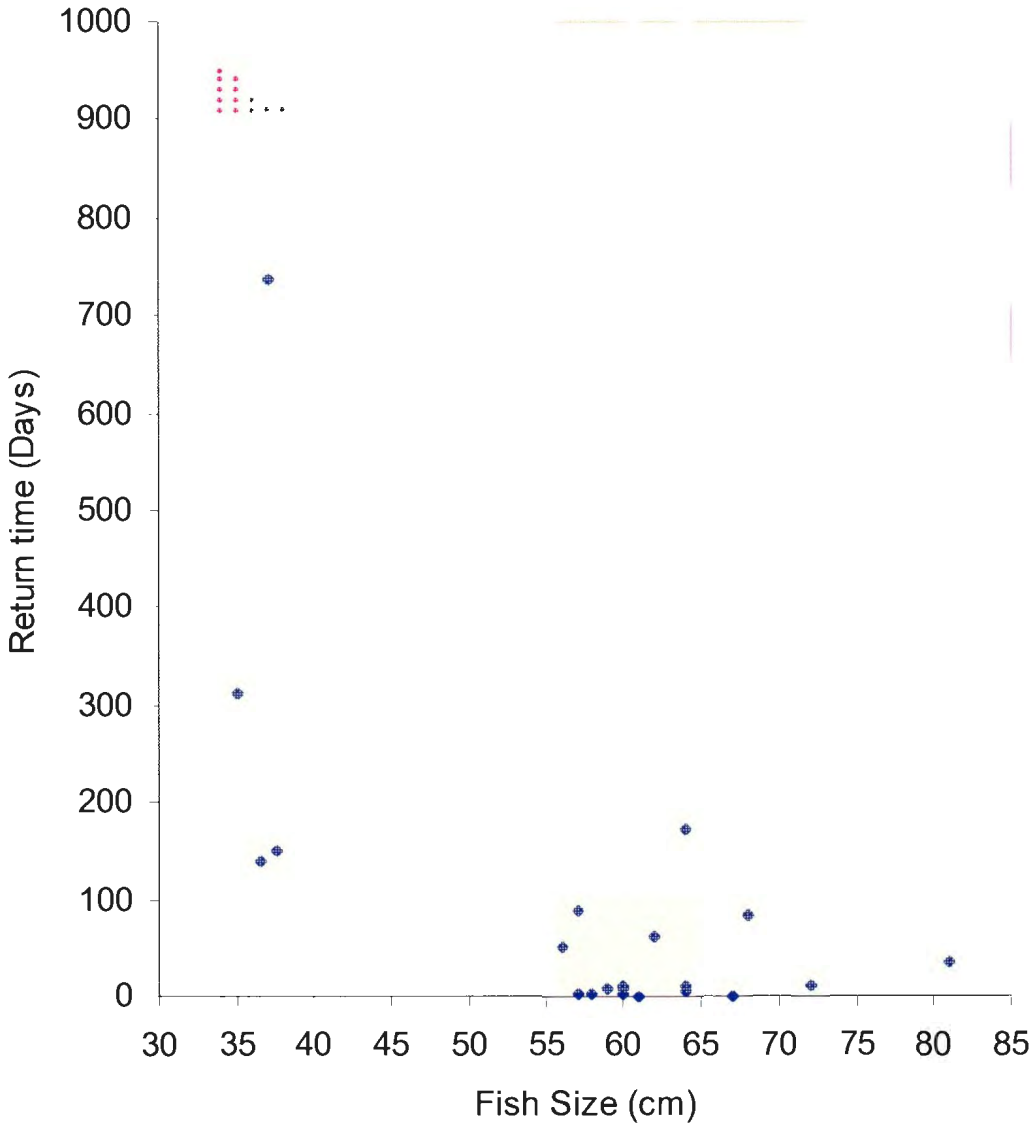
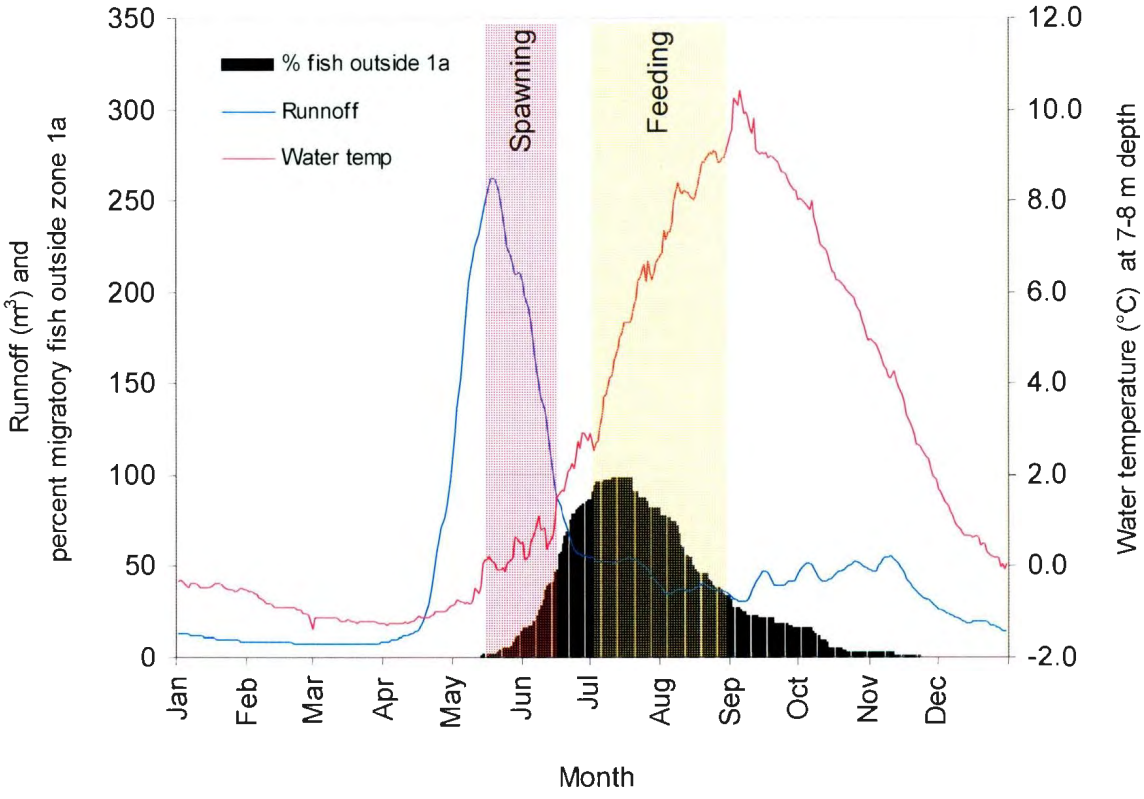

1000
900
800
700
600
500
400
300
200
100
0
Return time (Days)
30
35
40
45
50
55
60
65
70
75
80
85
Fish Size (cm)

Figure 4.12. Timing of spring freshet entering Gilbert Bay, summer water temperature at 8 meters depth in zone 1a, and migration of Gilbert Bay cod (out of and returning to the overwintering area) in relation to the spawning season and feeding season (time when capelin are available). The cod spawning period (see Chapter 2) is indicated in red and capelin availability (see Chapter 4; Templeman 1948) is indicated in Gray.

Figure 4.12


% fish outside 1a
Runnoff
Water temp
Spawning
Feeding
Runnoff ($m^3$) and
percent migratory fish outside zone 1a
Water temperature (°C) at 7-8 m depth
350
300
250
200
150
100
50
0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-2.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

# Chapter Five

# A temporally and spatially limited feeding migration by inshore Atlantic cod in Gilbert Bay, Labrador

## 5.1 ABSTRACT

During 2009-2011 the movements of resident inshore Atlantic cod were tracked continuously throughout their home range in Gilbert Bay, Labrador, using acoustic telemetry. Atlantic cod moved toward the coast, away from the overwintering and spawning areas at the head of Gilbert Bay, shortly before capelin arrived and returned after the capelin spawning season. During 2009, most migratory fish (15 of 21) were detected in close proximity to a capelin spawning site when capelin were spawning. Cod aggregated at the spawning beach for approximately two weeks during each of two discrete time periods in 2009. Each aggregation of Atlantic cod began to form on a full moon. The directional seasonal movement pattern towards the coast occurred during the same time and over similar distances each year. This small-scale summer feeding migration represents an important characteristic of the resident inshore Atlantic cod population in Gilbert Bay.

## 5.2 INTRODUCTION

Animal movement is a generalized term that refers to some activity on a local scale, whereas migration refers to a specialized behaviour that has its origin in natural selection (Tyus 2011). Animal migrations are diverse and have been interpreted in several different

ways, briefly described here but see Dingle and Drake (2007) for details. They describe migration as encompassing four concepts: (1) persistent locomotory activity, undistracted and straightened (2) relocation on a large scale over a longer duration than normal daily activities; (3) a seasonal to-and-fro movement between regions where conditions are alternately favorable or unfavorable (including one region in which breeding occurs); and (4) movements leading to redistribution within a spatially extended population. For the purposes of the current study, and in many studies of fish populations, migration follows concept 3 as outlined by Dingle and Drake (2007). Fish commonly exhibit migratory behaviour for feeding and spawning (Tyus 2011).

On both sides of the North Atlantic, Atlantic cod undergo well known large-scale feeding migrations, often in high abundances (Rose 2007; Bergstad et al. 1987). Cod typically spawn during winter and spring when feeding is reduced (Fordham and Trippel 1999) and subsequently migrate in search of prey. Although cod feed opportunistically on a wide variety of prey types (Scott and Scott 1988), they prefer fish prey but especially capelin (Lilly 1987; Bundy et al. 2000; Rose and O'Driscoll 2002; Sherwood et al. 2007), which some authors speculate may have contributed to their evolutionary success in colonizing offshore areas (Rose 2007). While many offshore cod migrate inshore, some smaller sedentary inshore groups of cod move only short distances seaward in search of food (Robichaud and Rose 2004; Rose 2007).

The local population of cod in Gilbert Bay exhibits a small home range and strong homing and site fidelity (Chapter 4). The core area for most of the population is likely

defined by MPA zone 1a (Morris and Green 2002, Chapter 4). During summer however, some Gilbert Bay cod move as far as 40 km from zone 1a, but return each fall (Chapter 4). This summer movement is consistently seaward, avoiding areas near the head of Gilbert Bay. This chapter describes observations of cod in relation to the occurrence of capelin along coastal areas from 2009-2011. Specifically, the hypothesis is that Gilbert Bay cod time their migration towards the coast in order to feed in more productive areas, where they prey upon schools of spawning capelin. The return migration of Gilbert Bay cod occurs soon after the capelin spawning season.

## 5.3 METHODS

Anecdotal observations on the occurrence of capelin in Gilbert Bay during 2009-2011, come from local residents of the community of Williams Harbour, located at the mouth of Gilbert Bay. Red Bay Beach (Figure 5.1) is well-known locally as a capelin spawning site where many local residents of Williams Harbour collect capelin during the spawning season for local use. Fortuitously, observations on capelin arrival dates during 2009-2011 were recorded in a log book kept at the local electrical power generation plant in Williams Harbour by the plant operators (Howard Russell and George Russell, residents of Williams Harbour). These operators also provided local knowledge on capelin. In 2009, a local aboriginal fishery guardian (Wayne Russell) monitored Red Bay Beach for capelin spawning activity in an effort to collect tissue samples as part of a capelin genetics study (Nakashima et al. in press).

Gilbert Bay cod movement was studied over several years using a network of acoustic telemetry receivers, as described in detail in Chapter 4. To detect the movements of ultrasonically tagged Gilbert Bay cod throughout their home range, multiple hydrophones were deployed throughout Gilbert and Alexis Bay, including one hydrophone near Red Bay Beach, where capelin are known to spawn. Details pertaining to hydrophones, numbers and types of ultrasonic tags, and surgical methodologies area described in detail in Chapter 4.

## 5.4 RESULTS

Interview information indicated that local residents harvest capelin regularly for food when capelin arrive at Red Bay Beach to spawn. During several years from 1992-2008, no capelin spawning occurred on Red Bay Beach and local residents often captured capelin elsewhere. When spawning did occur elsewhere during these years, abundances were low. During 2009-2011, capelin spawned on Red Bay Beach each year, and in relatively high abundances in 2010 and 2011 compared to 2009. Log book data and sample collections identified the onset of the capelin spawning season near Williams Harbour. Historically at least, local harvesters report that capelin spawn on Red Bay Beach more than once during the same season, described locally as the small run and large run (Wayne Russell personal communication).

Figure 5.1 indicates the dispersal area of migrating cod, tagged with ultrasonic transmitters, from zone 1a to other areas of the MPA and outside the MPA boundaries

during 2009-2011. Beginning on July 7th 2009, and for approximately two weeks thereafter, a single hydrophone located 1.5 km from Red Bay Beach detected the majority of migratory ultrasonically tagged cod in Gilbert Bay at a time when capelin were observed spawning. In 2009, 21 large cod migrated outside zone 1a and most (15 of 21) were detected at the capelin spawning location (Figure 5.2). The number of cod detected near the beach remained high for approximately two weeks and then decreased for approximately two additional weeks before detections at this location increased a second time. By August 4th a similar second peak in tagged cod numbers (13 of 21) occurred and then remained high for an additional 2-week period. Increased abundances of cod near the capelin spawning site in 2009 corresponded with a full moon (Figure 5.2). After the second peak in detections near Red Bay Beach, tagged fish moved back into zone 1a where they subsequently overwintered.

Although a similar aggregation of tagged cod was not detected at a specific location during 2010 or 2011 (Figure 5.2) when capelin abundance was high along the coast, tagged cod moved away from the overwintering area before the arrival of capelin and spent considerable time in coastal areas where capelin were reportedly abundant before returning to the overwintering site in zone 1a.

## 5.5 DISCUSSION

Gilbert Bay cod utilize coastal areas during summer, likely to access better foraging opportunities, resulting in a short summer feeding migration. Long-term sampling

conducted in zone 1a , at the head of Gilbert Bay, caught Atlantic cod almost exclusively, and very few other fish species were observed at this location (Chapter 2). Areas more toward the coast, including zone 3 and beyond support a comparatively diverse fish community including capelin and sandlance (Wroblewski et al. 2007). Feeding likely provides the impetus for the summer migration of Gilbert Bay cod.

In Labrador, Arctic charr (*Salvelinus alpinus*) conduct a short summer marine feeding migration from rivers, often located near the head of a fjord, to coastal areas (Dempson and Kristofferson 1987; Morris and Green 2012), not unlike the migration of Gilbert Bay cod. During the short summer growing season, a diet of capelin and other fish promotes faster Arctic charr growth than a diet of shellfish, suggesting that fish are an important and potentially preferred food source (Dempson 1995). Previous work showed that charr from Shinneys River migrated and foraged along the same coastal areas as those utilized by Gilbert Bay cod, avoiding the inner portions of Gilbert Bay (Morris and Green 2012). This pattern offers further evidence of improved feeding opportunities along the coast compared to the inner portion of Gilbert Bay.

Observations in 2009 captured an important interaction between cod and capelin that has never been recorded with such specificity, despite its ecological significance. Capelin spawning activity in Gilbert Bay began approximately July 6-8$^{th}$, 2009, corresponding with the full moon when higher tides may benefit capelin spawning (Templeman 1948; Nakashima personal communication). Cod moved away from overwintering areas during June, just prior to the arrival of capelin. The intense aggregation of migratory

ultrasonically tagged cod at the capelin spawning site also suggests that a large proportion of the entire migratory Gilbert Bay cod population was also present at this site in 2009, likely feeding on capelin.

A second aggregation of cod one month later again coincided with the full moon, suggesting capelin availability and a possible second capelin spawning event. Capelin were not specifically observed during the second aggregation of cod. However, in this and other areas capelin often spawn in two or more separate spawning events within a season (Nakashima 1996). Historically, capelin appear along the south coast of Labrador between June 28$^{th}$ – August 31$^{st}$ (Templeman 1948), which overlaps with the migration timing of Gilbert Bay cod to the coast (Chapter 4).

After the second aggregation at Red Bay Beach, Gilbert Bay cod dispersed and moved back to the overwintering area in zone 1a. The observations of the timing of cod migration towards the coast immediately after spawning (Chapter 4), the inshore migration and timing of capelin spawning during a full moon, and the degree to which cod aggregated to feed on capelin, provide an example of the complex ecological interaction that may occur between cod and capelin.

The mechanism cod use to locate capelin or other preferred food items is not well understood. Rose (1993) speculates that feeding migrations in Atlantic cod are partly learned (Rose 1993). Atlantic cod likely utilize vision and olfaction while foraging, which could also play roles in migration (Rose 1993; Tyus 2012). Data in Chapter 4

suggest the importance of individual experience in the migration of Gilbert Bay cod. Although speculative, it is possible that the experience of favorable feeding conditions at particular sites during migration could influence an individual's return to that area in the future. A specific analysis of individual movement patterns, particularly of juvenile fish with limited experience, could be extremely informative in better understanding how Atlantic cod learn and navigate. For example, smaller and presumably naive fish monitored during this study appeared to revisit familiar sites before moving to more distant new sites but detailed analysis of this specific behaviour requires more study.

The same intensity of aggregation was not observed among tagged cod at Red Bay Beach in 2010 and 2011; however, several ultrasonically tagged cod visited the site for at least a short time period. Local reports indicated that capelin were more abundant and wide spread in the area during 2010 and 2011, compared to 2009. It is suspected, although not confirmed, that capelin were less abundant and less widely distributed in 2009, concentrating cod as they followed capelin to the spawning beach.

## 5.6 CONCLUSION

The highly localized Atlantic cod population in Gilbert Bay resides in a small area (Chapter 3), however, a portion of the population migrates annually from core areas used during overwintering, spawning, and as a nursery area, towards the coast to feed. Cod avoid some areas of Gilbert Bay but use other areas extensively in summer but not in winter. This seaward migration suggests greater foraging opportunities near the coast during the short subarctic growing season. Observations of cod movement in 2009

suggest a potential link between the migration of ultrasonically tagged cod to the occurrence of capelin, a preferred prey item and potentially better feeding conditions.

The following chapter considers the spatial distribution and timing of migratory behaviour of Gilbert Bay cod in relation to the MPA boundaries and fishing seasons. Specifically, it addresses whether the migratory behaviour of cod to coastal areas outside the MPA increases cod vulnerability to capture during fishing activities that coincide with migration timing. This scenario could explain the population decline (Chapter 2), that raises concerns for management of the MPA. This information provides the basis for adaptive management decisions that could potentially improve MPA effectiveness.

Figure 5.1. Dispersal of migratory ultrasonically tagged cod from zone 1a. Figure includes only fish detected moving outside zone 1, represented by 100% detections at the exit of zone 1a. Scale (100%) is represented by a black bar at each receiver station. The full array of receivers was not established until 2009, so earlier data were therefore not included.

Figure 5.1

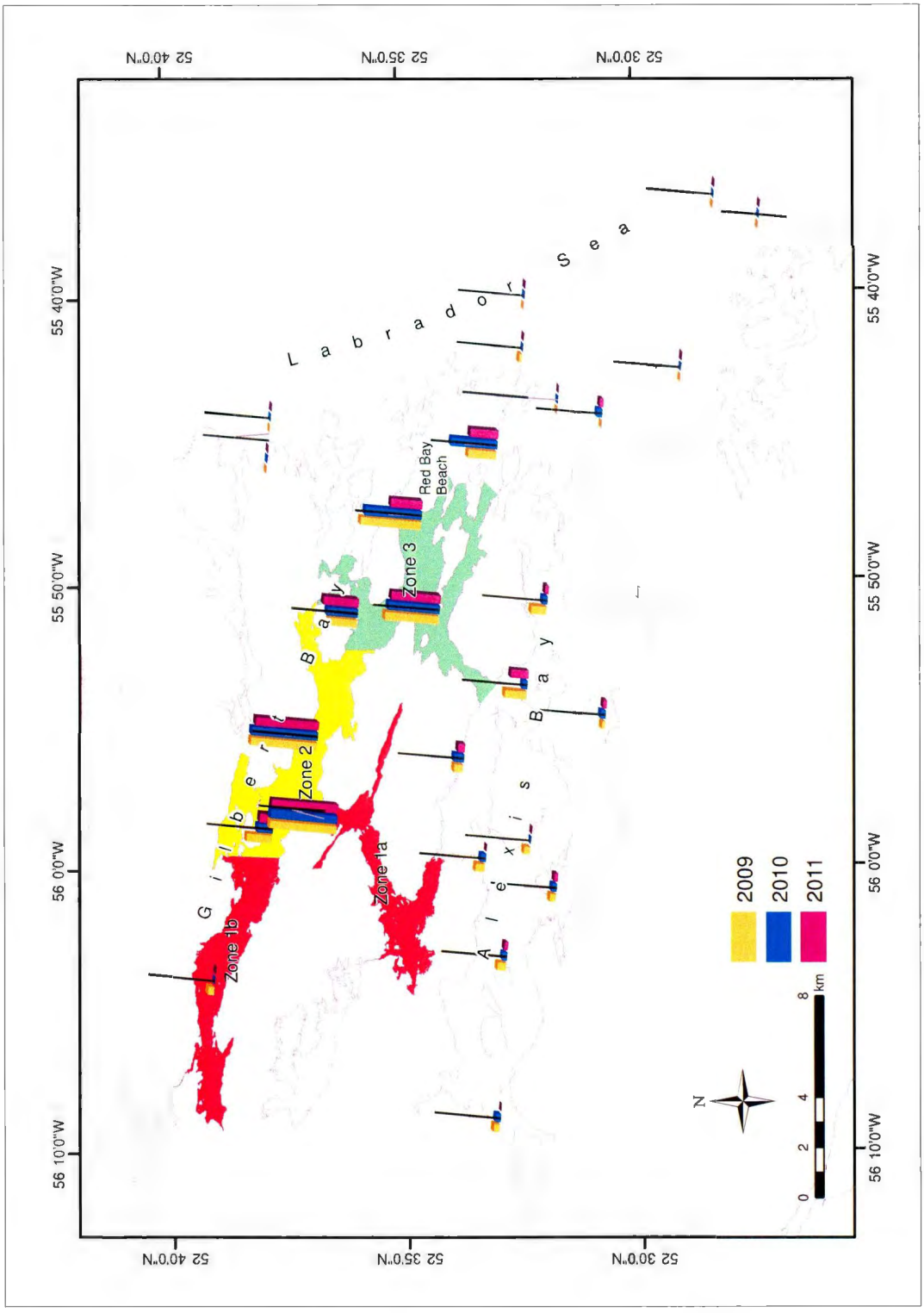
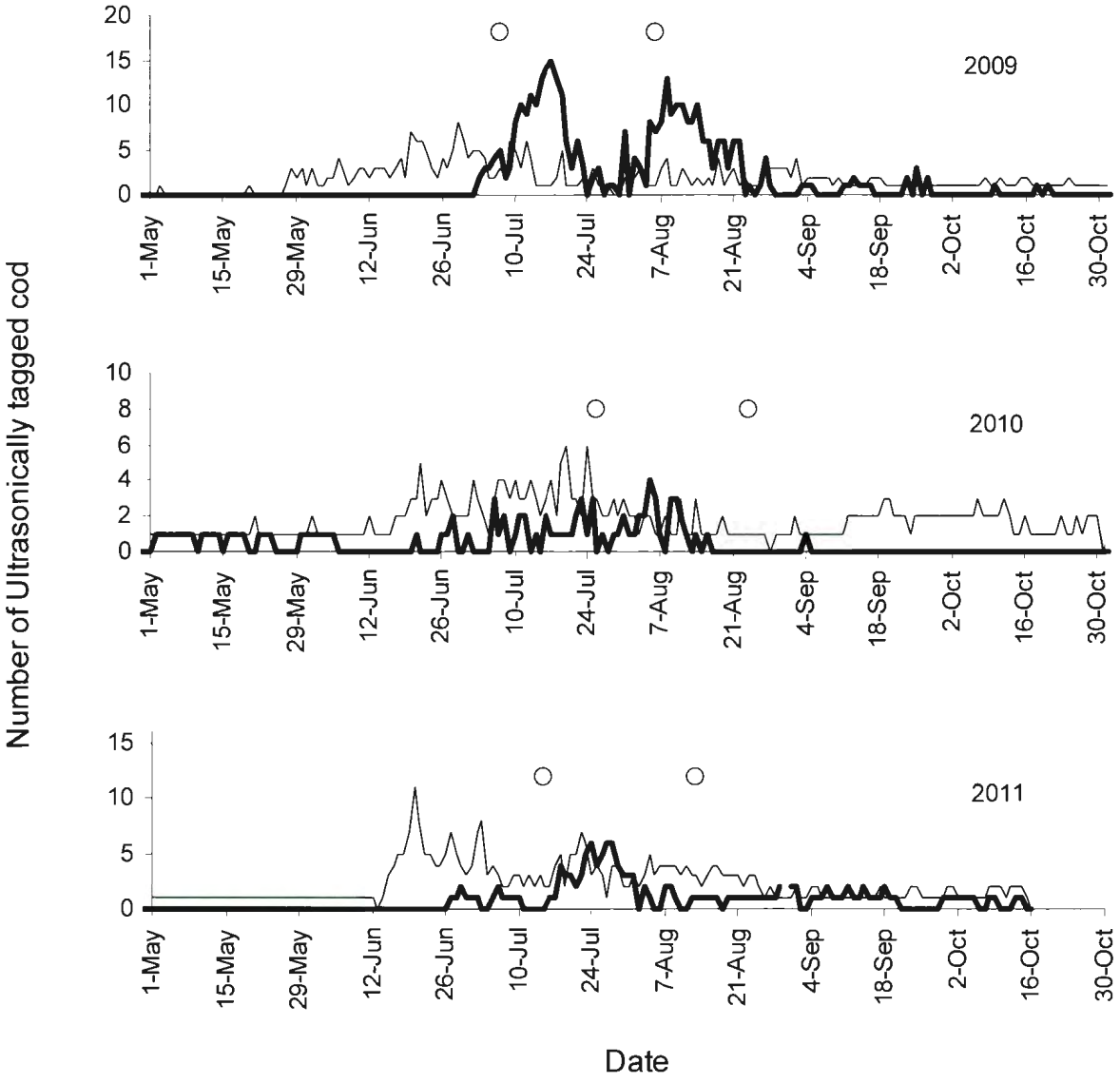

Labrador Sea
Red Bay Beach
Zone 1a
Zone 1b
Zone 2
Zone 3
Gilbert Bay
Alexis Bay
2009
2010
2011
N
0
2
4
8
km
52 40'0"N
52 35'0"N
52 30'0"N
55 40'0"W
55 50'0"W
56 0'0"W
56 10'0"W

Figure 5.2 Number of large cod (58-81 cm TL) with sonic tags detected per day during the summer migratory period, at stations located outside zone 1a, 2009-2011. The black line represents tags detected at 1 station near Red Bay Beach, while the shaded area represents the number of fish detected per day at all other 18 monitoring stations outside zone 1a. Open circles indicate the date of the full moon. Tags available include 28 in 2009, 34 in 2010 and 34 in 2011.

Figure 5.2


Number of Ultrasonically tagged cod
2009
2010
2011
Date
1-May
15-May
29-May
12-Jun
26-Jun
10-Jul
24-Jul
7-Aug
21-Aug
4-Sep
18-Sep
2-Oct
16-Oct
30-Oct

# Chapter Six

## Adaptive management to improve MPA efficacy

### 6.1 ABSTRACT

Although an important conservation tool, Marine Protected Areas sometimes fall short of intended goals. Efforts to develop an MPA in Gilbert Bay, Labrador, Canada, began in 1998 as a precautionary measure to protect a unique Atlantic cod population and its habitat from overfishing. Despite MPA measures the cod population decline continued, requiring adaptive management to protect the Gilbert Bay cod while they are susceptible to fishing in areas outside the MPA. Acoustic telemetry and external tagging was used over several years of monitoring to determine when cod moved outside the MPA, the duration of time outside, distance moved, and when fish returned. Fishing seasons overlapped with the time Gilbert Bay cod move outside the MPA. Public consultations and a phone survey with Atlantic cod harvesters suggest that changing the fishing season would not have a significant adverse affect on commercial fishing. To increase MPA efficacy, an adaptive management strategy that changes the commercial fishing season to a period when Gilbert Bay cod are inside the MPA is recommended. However, because unplanned changes to MPA regulations are difficult to implement in established MPAs, future MPA planning should recognize that adaptive management strategies may be necessary if an MPA is to achieve its objective.

## 6.2 INTRODUCTION

Marine Protected Areas (MPAs) represents a potentially important fisheries management tool worldwide (Agardy 1994; Pauly et al. 2002; Roberts et al. 2005), garnering significant international commitments (CBD 2006; Wood et al. 2008) that ensure their continued implementation into the foreseeable future. The umbrella term MPA can include a variety of spatial management measures that completely or partially protect an area from a variety of activities. Because ill-considered MPAs may be detrimental (e.g. Mullowney et al. 2011) it may be misleading to promote them as devices which are always likely to improve yields (Hilborn et al. 2004). As Marine Protected Areas become increasingly popular, evidence suggests that not all will be successful (Agardy et al. 2011), emphasizing the importance of improving MPA effectiveness when problems are identified and thus invoking adaptive management. Adaptive management refers to the systematic acquisition and application of reliable information to improve natural management over time, which has been promoted as essential to management under uncertainty (Wilhere 2002). For MPAs to be an effective fishery management tool they must be examined on a case by case basis, with due consideration being given to the spatial connectivity of larval dispersal, juvenile and adult swimming, and activities of fishermen (Hilborn et al. 2004; Botsford et al. 2009).

Substantial declines in the Gilbert Bay cod population occurred while the population was under MPA protection, apparently from fishing and variable recruitment (Chapter 2). Gilbert Bay cod begin to seasonally migrate outside the MPA and into commercial fishing areas as they reach sexual maturity, at sizes greater than 35 cm total length (5+ yrs

old) (Chapter 4). However, recruitment to a size vulnerable to typical fishing gear (gillnets) only occurs at 45 cm and approximately 7 year of age. Fishery removals of strong year classes, followed by several years of poor recruitment has resulted in low overall biomass and abundance of commercial size Gilbert Bay cod (Chapter 2).

Although multiple researchers tout MPAs and MPA networks as a means to ensure old-growth age structure and complex spatial structure in populations of ground fish (Berkeley et al. 2004; Baskett et al. 2005), not all MPAs prove successful. However, given the considerable cost and efforts necessary to create and maintain MPAs (Balmford et al. 2004), and because they represent an important future management tool (CBD 2006), efforts should prioritize identifying means to improve current and future MPAs. Given the potential for MPA shortcomings, MPA implementation should be guided by the scientific principles of adaptive management: experimental treatments, controls and evaluation (Walters 1986; Hilborn et al. 2003).

Evidence from science monitoring and community consultations was used to describe a potential adaptive management strategy to improve MPA efficacy in Gilbert Bay. Consideration of specific harvest control rules, in consultation with local stakeholders, could help prepare managers to implement effective changes quickly. Recognizing management problems and adopting science-based changes to correct or minimize them could represent a prudent adaptive management strategy in the case of Gilbert Bay's MPA.

## 6.3 METHODS

### 6.3.1 Acoustic telemetry

The Gilbert Bay Marine Protected Area boundaries extend approximately 20 km from zone 1a, which is a core area for much of the population that is particularly important for overwintering and spawning. The movement patterns of small non-commercial (<40 cm), and larger commercial (58-75 cm) sized fish were contrasted using tagging and tracking methodologies described in Chapter 4. To examine the potential effects of fish movement in relation to MPA boundaries, acoustic telemetry data described in chapter 4 was re-analyzed considering only migratory fish and then grouped in relation to MPA boundaries, considering how far migratory fish moved and when they returned to the MPA.

### 6.3.2 Interview survey

The results of a telephone survey contracted by DFO regarding the commercial cod fishing season in southern Labrador, were discussed at a public MPA meeting held in Port Hope Simpson on March 7$^{th}$, 2012, and those results are summarized here. The DFO survey questions are included in appendix 1 of this thesis. The survey was contracted to a group outside DFO and conducted during fall of 2011, through interviews with 47 commercial Atlantic cod fishermen representing 34% of all commercial license holders along the southern coast of Labrador. The survey areas considered the area from Black Tickle in the north to Mary's Harbour in the south. Based on cod tag returns and acoustic

telemetry (Chapter 4) 16 of 47 people interviewed fished in areas frequented by Gilbert Bay cod. During the survey, Atlantic cod fishermen were asked if they would be negatively affected by limiting the commercial fishing season between September 7$^{th}$ and October 7$^{th}$, and between September 15$^{th}$ and October 15$^{th}$.

## 6.4 RESULTS

Large Gilbert Bay cod leave the MPA between July and early September, and some individuals do not return until October (Figure 6.1). Small fish leave the Marine Protected Area during summer (July – September) and return to the MPA by late September (Figure 6.2). The time spent ouside the MPA each year lasted less than 2 months (Figure 6.3). Thus, most large and small fish returned to the MPA by mid-September (Figure 6.3). A low proportion of fish with ultrasonic tags were detected at single hydrophone stations outside the MPA, indicating that fish generally spread over wide areas outside the MPA (Figure 6.4). Most fish that migrated from the spawning area travelled to zone 3 or within about 10 km of existing MPA boundaries (Figure 6.5). Very few fish were detected at the furthest hydrophones after they were deployed in 2008, suggesting that few fish move this great a distance. More fish were detected by hydrophones located outside, but geographically closer to MPA boundaries.

The timing of commerical fishing and individual quotas varied since 1998 (Table 6.1), but comprised the largest known source of fish removals in the vicinity of Gilbert Bay. In some years the commercial fishing season included separate summer and fall components. As a conditions of their commercial license, fishermen are required to

participate in the collectection of fishery data, such as dock-side monitoring of their catch.

Of the 47 participants in the phone survey, 65% indicated no negative impact of a September 7th - October 7th season, and 57% indicated no negative impact of a September 15th - October 15th season. Harvesters preferred an early fall fishery, because poor weather in late fall could limit fishing opportunities.

## 6.5 DISCUSSION

Given that Gilbert Bay cod moving outside the MPA may be removed by commercial fishing; changes to the timing or location of fishing activities could improve MPA effectiveness. MPA consultations during 2008 and 2009 indicated little support for changing the boundaries of the MPA (Jennifer Janes, DFO Marine Protected Areas program coordinator, personal communications). Boundaries were initially determined through an extensive consultation process that incorporated scientific advice (Morris and Green 2010) and was agreed upon by stakeholders during an eight year period before the MPA was established in 2005. Given that multiple stakeholders, including fish harvesters, do not support changes to the MPA boundaries, this strategy represents an unlikely option at this time. However, the exploration of changes to the fishing season appears more favorable among stakeholders as a means to improve MPA effectiveness.

For rebuilding to succeed, managers must work together in using various tools provided by both the Oceans Act and Fisheries Act to identify and address periods of vulnerability through flexible adaptive management decisions. Restricting fishing activities in the

vicinity of Gilbert Bay until cod return to the MPA will better protect the Gilbert Bay cod population. Based on fish movement patterns in relation to the timing of commerical fishing, commercial fishing from July until September likely has the largest impact on Gilbert Bay cod. The 2007 fishery, conducted from July 23-August 4 caught nearly 18,000 kg of Atlantic cod, and likely had the largest impact on Gilbert Bay cod in recent years. The largest decrease in spring scientific catch rates, based on monitoring data, occurred between 2007 and 2008, which included the 2007 commercial fishing season (Chapter 2).

Harvesters reported availability of northern cod, the targeted commercial stock of Atlantic cod fished in the vicinity of Gilbert Bay, during the fall in recent years and have fished commercially during this time period. Therefore a successful fall fishery is a realistic strategy with a proven track record. A fall fishery would enable Gilbert Bay cod to migrate outside the MPA during summer and return to the MPA without impact by commercial fishing. A later season could therefore represent an effective adaptive management policy to help the Gilbert Bay cod population rebuild.

In our experience, stakeholders, managers and scientists recognized problems related to the effectiveness of the Gilbert Bay MPA since 2008, and in 2010 sufficient data were available to formally describe them (Morris and Green 2010; DFO SAR 2010). Initial suggestions in 2009 to alter the MPA boundary as a means to protect fish that moved outside the MPA received limited support. Therefore, in 2010 researchers suggested that changing the fishing season could improve MPA efficacy. Management actions often

take considerable time. MPAs are not independent of other harvest control rules (Hilborn 2002; Halpern et al. 2004) and should not be expected to work as an isolated strategy. Therefore, additional or alternative harvest control rules should be considered during MPA planning to reduce required implementation time and ensure stakeholders are informed of potential management actions if MPA goals are not met. If fishers are made aware early in the process of potential and sometimes temporary rule changes that either increase or decrease access may be necessary in order to meet MPA objectives then they may be more willing to consider such actions should they become necessary. Without such planning and future flexibility, the likelihood of an MPA achieving its objectives may be compromised.

Several sources other than commercial fishing may contribute to Atlantic cod fishing mortality in the vicinity of Gilbert Bay, including directed recreational and aboriginal fishing for Atlantic cod and by-catch during charr and salmon gillnet fishing. The relative importance each of these sources of mortality is difficult to measure and data exist only for commercial fishing, with little information describing catch and effort from the other fisheries. Since 2007, the recreational cod fishery has included a 3-4 week period in late July and first half of August and a second shorter (9 day) period in late September-early October. Recreational fishing is not permitted inside the MPA at this time because the population is at a low level; should the population increase in abundance, MPA regulations allow recreational fishing in MPA zone 3 (Canada Gazette 2005). The recreational catch estimate reported in Morris et al (2003) during 1999 was just one ton, much less than commercial reported landings from that area. Directed aboriginal cod

fishing is typically a communal harvest with dedicated harvesters. Reportedly, the local harvesters have caught cod allocations from areas outside the range of Gilbert Bay cod (Wayne Russell, NunatuKavut fishery guardian, personal communication). Ther is no information available describing by-catch of cod during salmonid gillnet-fishing. Regardless of its source, fishing mortality on Gilbert Bay cod is currently more problematic than in the past because population abundance has dropped to such low levels. Improved data collection during other fisheries could help to understand better the fishing pressure on the cod population and assist with its future management. Currently, however, population rebuilding for Gilbert Bay cod requires additional restrictions to reverse this decline.

## 6.6 CONCLUSIONS

The Gilbert Bay MPA has partially fulfilled its mandate of protecting the local cod population and its habitat (Chapter 2). The MPA protects the most important spawning area (Chapter 3) and a large portion of the population's migratory range (Chapter 4). Without this protection the population would likely have experienced direct fishing pressure within its core areas, as it did during 1998 and 1999 (Morris and Green 2002; Morris et al. 2003), resulting in catches comprised almost entirely of Gilbert Bay cod. This pressure would have resulted in considerably larger declines. However, information provided by scientific monitoring and research suggests that the MPA can be much more effective through implementing the suggested adaptive management decisions. Because Gilbert Bay cod migrate a short distance outside the MPA during a short time period in

summer, delaying the annual fishery within a relatively small spatial area until a time when Gilbert Bay cod return to the MPA could provide a potentially valuable adaptive management measure.

Table 6.1. Commercial Atlantic cod catches (round weight) reported by Department of Fisheries and Oceans dockside monitoring program at locations where tagged Gilbert Bay cod were caught. Fishing areas encompass headland areas from Salmon Point (N 52° 37. 44, W 055° 44. 51) in the north, to Cape Spear (N 52 26 35, W 055 37 38) to the south, and all of Alexis Bay. The northern cod fishery was closed from 2003-2005.

| Year | Fishermen | Catch (kg) | IQ (kg) | % quota Caught | Season dates |
|---|---|---|---|---|---|
| 1998 | 12 | 8,135 | 1125 | 60 | September 24- October 16 |
| 1999 | 11 | 12,057 | 4082 | 27 | July 8-31 and September 13 – October 16 |
| 2000 | 3 | 613 | 3810 | 5 | June 16 – July 19 and September 11 – November 30 |
| 2001 | 2 | 928 | 3810 | 12 | July 9 – September 30 and November 5 – 30 |
| 2002 | 9 | 5,740 | 3810 | 17 | July 30 - October 13 |
| 2003 | No Fishery | | | | |
| 2004 | | | | | |
| 2005 | | | | | |
| 2006 | 10 | 6,598 | 1361 | 48 | August 16 – September 22 |
| 2007 | 19 | 17,672 | 1134 | 82 | July 23 – August 4 |
| 2008 | 23 | 17,631 | 1474 | 67 | September 8 – 6 October |
| 2009 | 17 | 14,385 | 1700 | 50 | September 7 – October 3 |
| 2010 | 14 | 11,500 | 1700 | 48 | August 28 – October 1 |
| 2011 | 11 | 9,400 | 1700 | 50 | August 29 – September 25 |

Figure 6.1. Cumulative percentage of ultrasonically tagged large cod that moved from (left) and cumulative percentage that returned to (right) the MPA. Top panels show data from 2009 to 2011, and bottom panels combine these data to indicate the general timing of large fish moving outside and inside the MPA, which extends approximately 20 km from zone 1a.

Figure 6.1

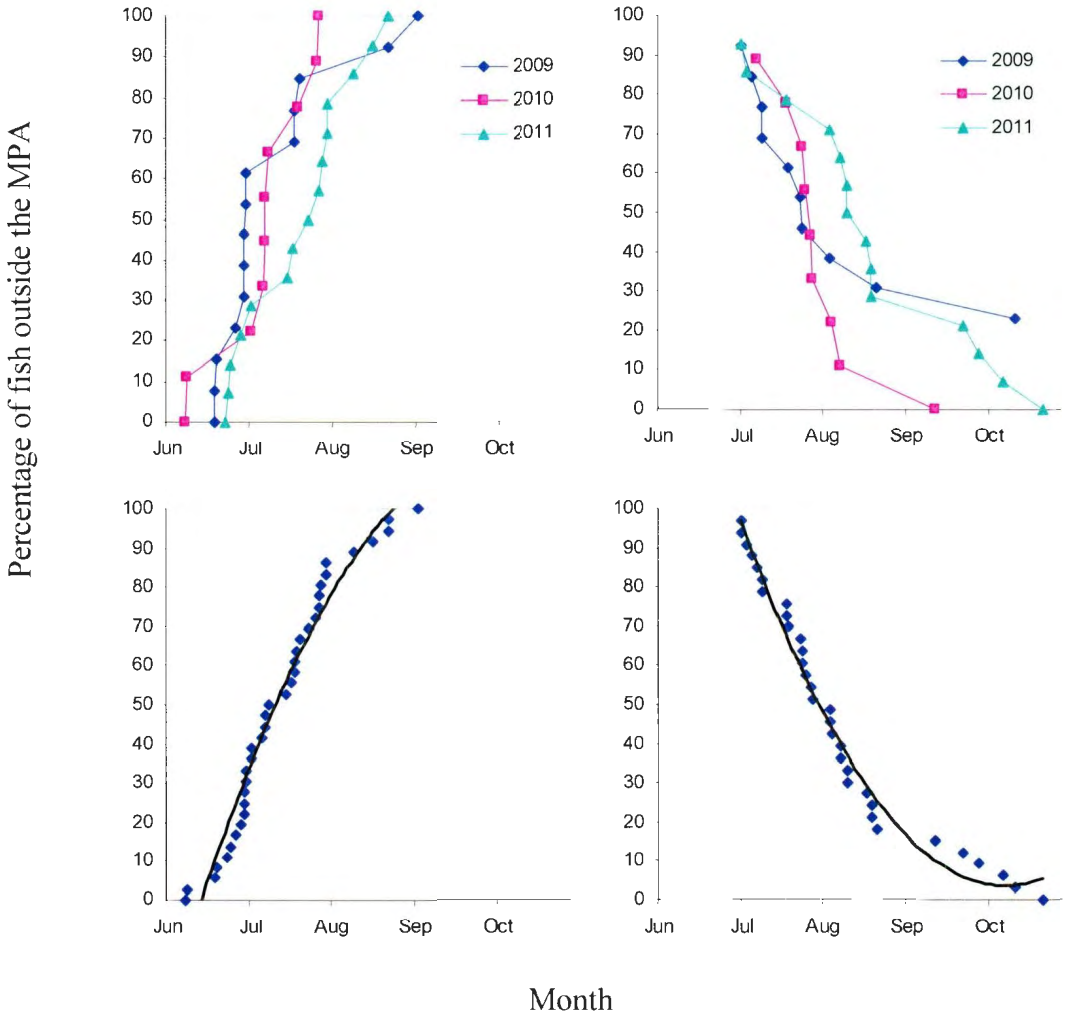

Percentage of fish outside the MPA
100
90
80
70
60
50
40
30
20
10
0
Jun
Jul
Aug
Sep
Oct
2009
2010
2011
Month

Figure 6.2. Cumulative percentage of ultrasonically tagged small fish that moved from (left) and cumulative percentage that returned to (right) the MPA. Top pannels show data from 2010 and 2011, and bottom pannels combine the data to indicate the general timing of small fish movements from and returning to the MPA, which extends approximatley 20 km from zone 1a. Ten small fish were tagged in 2009 but were smaller than migratory size in that year.

Figure 6.2

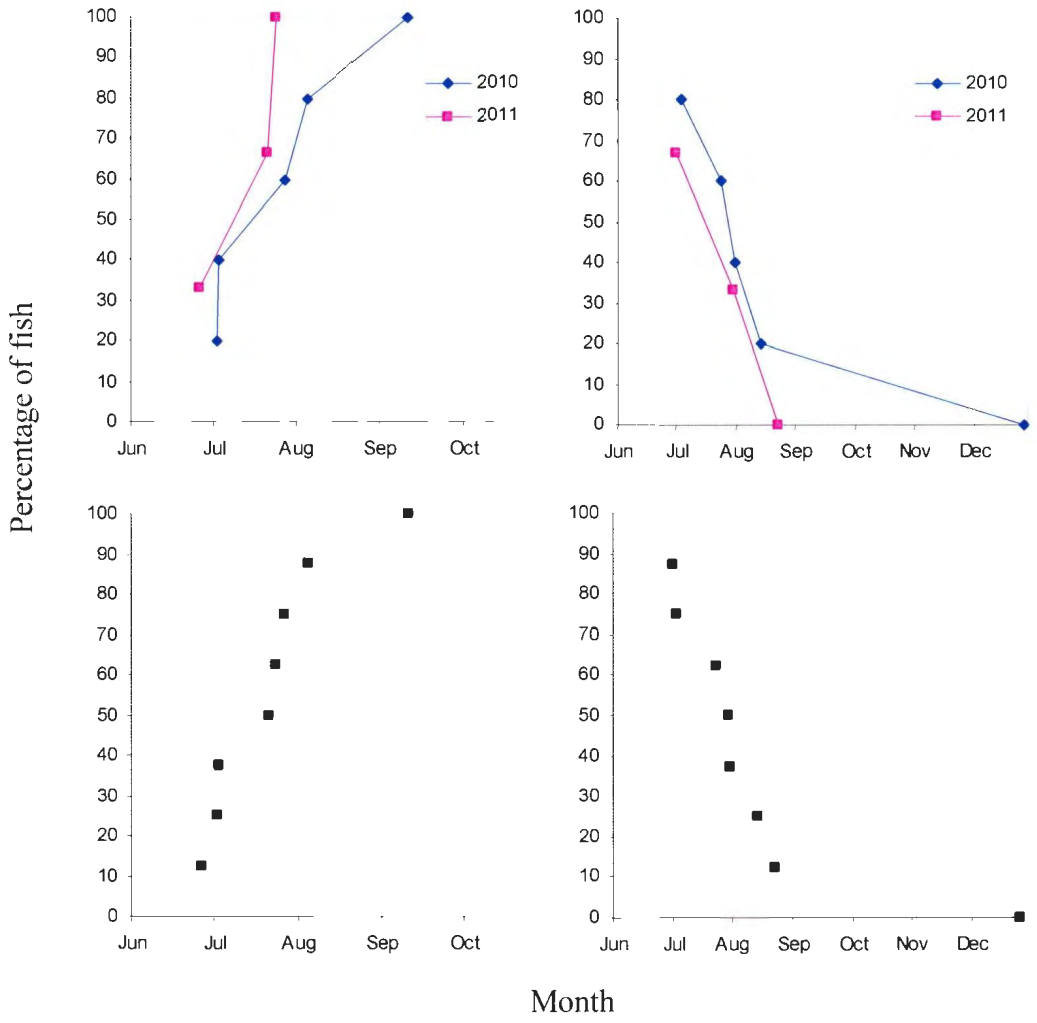
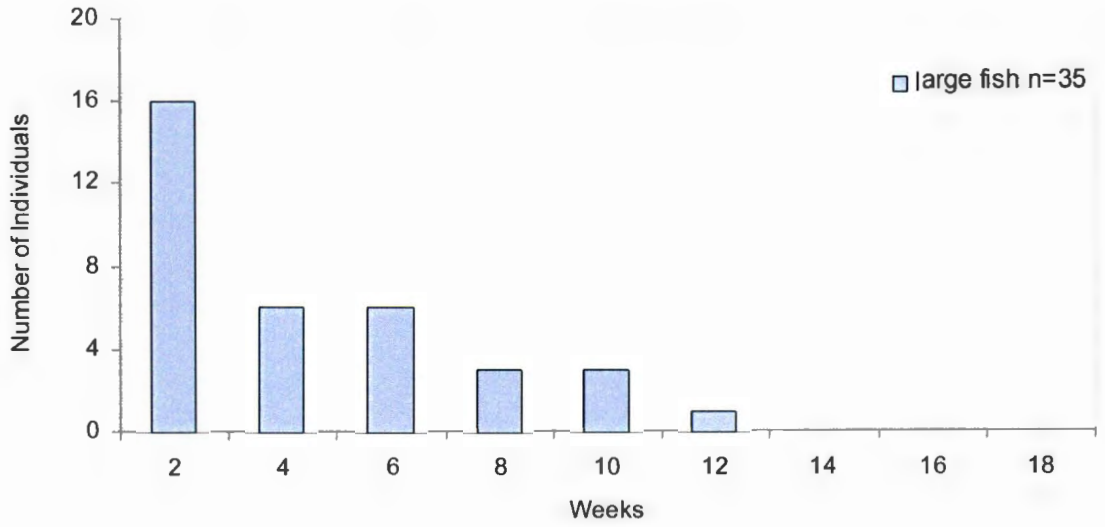

Percentage of fish
100
90
80
70
60
50
40
30
20
10
0
Jun
Jul
Aug
Sep
Oct
Nov
Dec
2010
2011
Month

Figure 6.3. Duration of time that large fish (top) and small fish (bottom) spend outside the MPA, before returning to zone 1a annually. No small fish moved outside the MPA in 2009.

Figure 6.3


20
16
12
8
4
0
Number of Individuals
large fish n=35
2
4
6
8
10
12
14
16
18
Weeks

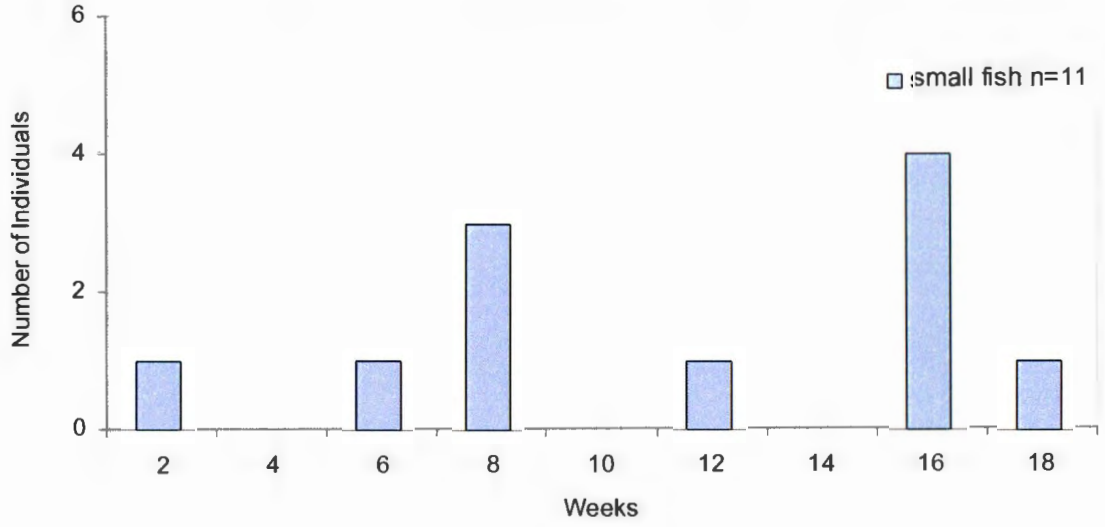

6
4
2
0
Number of Individuals
small fish n=11
2
4
6
8
10
12
14
16
18
Weeks

Figure 6.4. Map of areas where ultrasonically tagged migratory cod moved during summer. Coloured bars denote the percentage of fish detected at each receiver station during each year of migration (2009-2011). Scale (100%) is represented by a black bar at each receiver station. The full array of receivers was not established until 2009, so earlier data were therefore not included.

Figure 6.4

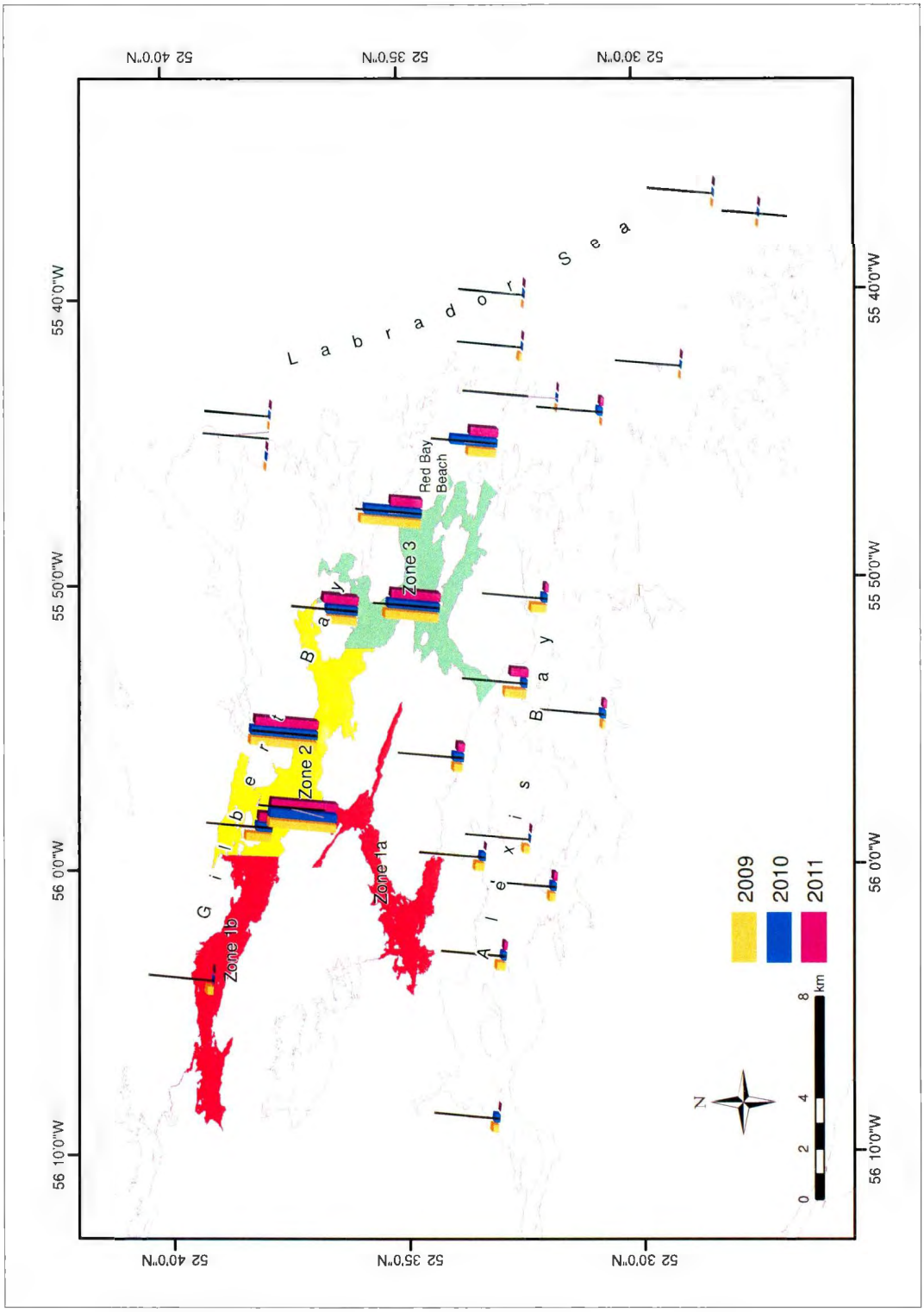
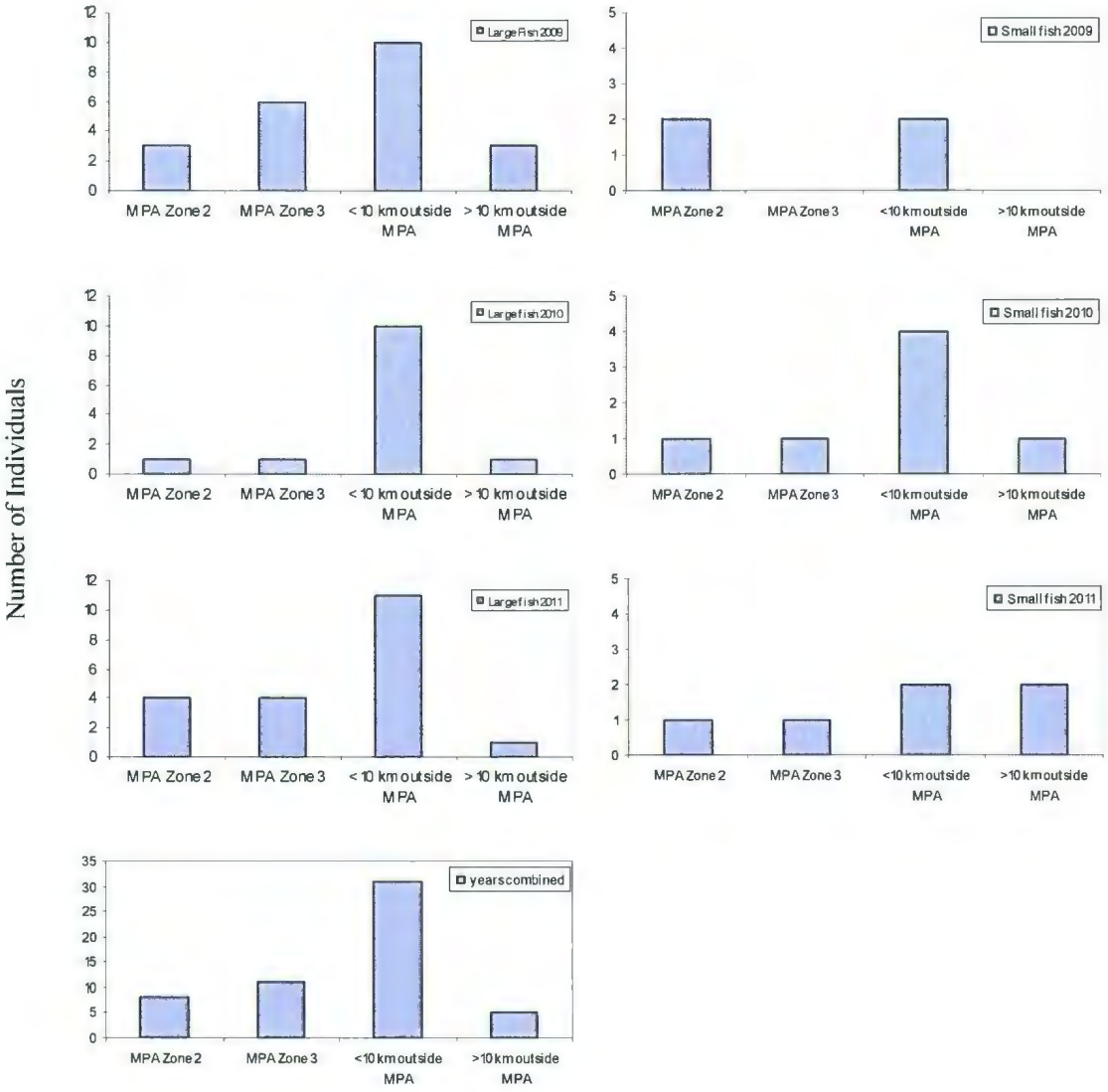

Labrador Sea
Red Bay Beach
Zone 1a
Zone 1b
Zone 2
Zone 3
2009
2010
2011
km
0
2
4
8
N
52 40'0"N
52 35'0"N
52 30'0"N
55 40'0"W
55 50'0"W
56 0'0"W
56 10'0"W

Figure 6.5. Distribution of the estimated maximum distances travelled by large (left) and small (right) fish that moved away from zone 1a. Distances increase in approximately 10 km intervals.

Figure 6.5


Number of Individuals
Large Fish 2009
Small fish 2009
Large fish 2010
Small fish 2010
Large fish 2011
Small fish 2011
years combined
MPA Zone 2
MPA Zone 3
< 10 km outside MPA
> 10 km outside MPA
<10 km outside MPA
>10 km outside MPA

## Chapter Seven

## Conclusions

Multiple studies have documented inshore Atlantic cod populations throughout the species' range, particularly along the coast of Norway. Some of these reports suggest that areas of the western Atlantic once supported a greater number of inshore Atlantic cod populations than currently exists, including areas in Maine (Ames et al. 1997, 2004), and along the coasts of Newfoundland and Labrador (Myers et al. 1997; Rose 2007). In some cases, these populations were likely overharvested and wiped out (Myers et al. 1997; Ames et al. 1997, 2004). The persistence of some local inshore populations during periods when historically larger offshore populations in the Newfoundland and Labrador region failed to rebuild further emphasizes the importance of inshore populations, and the need to protect and conserve biocomplexity in the face of ongoing threats such as fishing.

Gilbert Bay supports a unique, well-defined coastal Atlantic cod population that appears to display local adaptation to its environment and behavioural attributes that distinguish it from other Atlantic cod populations. During this long-term study, research identified a decline in the population since the Gilbert Bay MPA was implemented in 2005. A need to improve the efficacy of the Gilbert Bay MPA emerged. Further research evaluated elements of population connectivity and potential ways to improve MPA effectiveness. A consistent spawning location and spawning period linked to physical attributes that increase egg and larval retention suggests low connectivity of this population to others, and that changes in spawning location or dispersal did not contribute to variable recruitment patterns. Strong homing and site fidelity of both juveniles and adults further

reduced the connectivity of this population with others. More specifically, this study documented the timing and spatial distribution of Gilbert Bay cod, which includes areas outside the MPA where commercial fishing has likely affected the population's abundance.

This research identified potential ways in which adaptive management could be applied to improve the effectiveness of the Gilbert Bay MPA by drawing on increased understanding of the population's connectivity. Field studies of this type are necessary to identify potential sources of biocomplexity that could benefit from specific conservation efforts to help sustain healthy aquatic living resources. The Gilbert Bay Marine Protected Area was established to achieve just this very objective for the local cod population.

Fisheries management must consider population complexity in decision making (Stephenson 1999; Sterner 2007; Reiss et al. 2009). Establishing an MPA in Gilbert Bay helped to protect the local cod population which likely would have declined much faster in the absence of the MPA, however the efficacy of the MPA can be improved. This study suggests that changes to seasonal commercial fishing dates could enable large Gilbert Bay cod to return to the MPA before the start of commercial fishing, and thus help to conserve the local Atlantic cod population. Progress toward implementing adaptive management solutions has been slow; it took eight years to designate the MPA and four years have passed since concerns regarding populations abundance and demographics were recognized (DFO 2010). To avoid such delays in taking action in future and to expedite the process, potential alternative management options should be

considered during MPA planning and long-term monitoring, so that stakeholders are well informed of potential management actions should an MPA fall short of its goals and objectives.

Understanding why some fish populations do not recover after collapse remains a challenge for fisheries research. ICES (2007) and Petitgas et al. (2006) provided circumstantial evidence that learning could play a role in maintaining fish populations for multiple species including clupeids, tuna, striped bass and whiting, suggesting that long delays in the return of historical migratory patterns within populations may result from the loss of experienced fish. Such behavioural considerations have received relatively little attention as an important component in the persistence and rebuilding of collapsed or depleted populations; rather management efforts have focused on monitoring and responding to trends in biomass or abundance (see Fogarty and Murawski 1998; Hutchings 2000). Abundances of migratory populations typically exceed (often more than ten times) those of resident populations within and between related species (Fryxell et al. 1998), presumably because reproductive and/or feeding benefits offset the energetic costs of migration. In some species, the loss of migration precedes dramatic population declines or local extinctions (Bolger et al. 2008; Newmark 2008). Petitgas et al. (2010) suggest that loss of structural elements related to life-history diversity, and loss of socially transmitted behaviour (through a curtailed age range) could limit recovery of depleted populations. Although our study did not test social transmission of knowledge, it identified the importance of experience to navigation and migration for the Gilbert Bay cod population.

The increasing rate of anthropogenic impacts of marine environments over multiple spatial scales emphasizes the urgent need to sustain biological diversity and protect the ecological and evolutionary processes that sustain and generate diversity (Moritz 1994; Cowling & Pressey 2001; Olsen et al. 2008). Areas that exhibit local adaptations and diversity, and add biocomplexity, can help maintain healthy and resilient ecosystems (Hilborn et al. 2003; Schindler et al. 2010). This need is particularly relevant if differences among populations result largely from phenotypic plasticity, in which case changes in behaviour or increased straying could contribute to the rebuilding of other depleted populations. Within salmonids at least, changing environmental conditions can change phenotypes and lead to modified migratory behaviour (Jonsson and Jonsson 1993; Olsson et al. 2006). Rose (2007; Rose et al. 2011) speculated that changes in behaviour of cod could explain the occurrence of an inshore cod aggregation in Smith Sound, Newfoundland, which persisted for more than a decade since 1995. Moreover, individuals from that population perhaps always have been and could be once again connected with offshore regions to contribute to future offshore production (Rose 2012; Brattey personal communication). If such connectivity and variability among populations exists, it further validates the need to establish inshore MPAs as a tool to encourage a more rapid rebuilding of other populations, including those in offshore areas. Although this spillover benefit appears unlikely for Gilbert Bay cod given its genetic distinctiveness (Bradbury et al. submitted), local adaptations and population specific characteristics, it nonetheless contributes to regional biocomplexity. Moreover, the future

of this population and its role in regional metapopulation structure is unpredictable given rapid changes in climate in the north that may influence populations in myriad ways.

Morphology, behaviour, physiology, genetics, or life history can define distinct populations (Taylor 1991; Marcil et al. 2006). However, a significant challenge remains in separating genetic from environmental influences on phenotypic variation (Olsen et al. 2008). Nonetheless, conservation of biocomplexity and intraspecific diversity hinges on identifying these differences (Hilborn et al. 2003; Schindler et al. 2010). In the absence of common garden experiments, genetic evidence coupled with field observations can identify potential local adaptations to advise conservation efforts based on a precautionary approach, until the technology necessary to link genes to phenotypic differences, and thus identify local adaptation, becomes readily available.

Ciannelli et al. (2010) asked "why has local population structure of Atlantic cod evolved and what might be the fitness advantage of fjord-specific home ranges?" Typically, inshore populations migrate less than offshore populations. Migration can be partly explained by a tradeoff between migration costs and benefits of not migrating (Finstad and Hein 2012) and should be favoured when the use of multiple habitats improves lifetime fitness (Gross et al. 1988). Short (less risky) migrations could be advantageous during periods of reduced food supply, and under these conditions non-migratory populations located in more productive coastal areas would likely experience higher growth rates and lower mortality (better overall fitness) than migratory populations that spend considerable time in areas of lower productivity. This study, and similar telemetry

studies conducted in Newfoundland fjords (Brattey et al. 2008) showed low rates of mortality ($Z<0.2$) compared to mortality estimates for cod ($M=0.5$) in offshore areas (DFO 2012). The expected mortality rates for cod in offshore areas are blamed for continued low levels of abundance and growth in this area (DFO 2012). Coastal areas are among the most productive regions of the ocean, typically with higher concentrations of potential prey than adjacent offshore waters (Denman and Powell 1984; Rissik et al. 1996). Coastal residency of Atlantic cod could represent a successful strategy, compared to large-scale offshore feeding migration, given the recent (two decades) population structure of cod in offshore areas and low abundance of capelin and other prey.

The Gilbert Bay population clearly exemplifies the susceptibility of local inshore populations to overharvesting when managed under broadly applied fishing regulations inappropriate to the scales of population connectivity. Connectivity, which may involve egg and larval transport and retention and/or specific adult behavior, clearly helps define the small spatial scales at which independent populations exist. Management strategies such as MPAs can protect diversity, but to do so effectively requires understanding population connectivity, often at small spatial scales (km to 100s of km), and implementing adaptive management decisions when scientific advice deems such actions necessary. This long-term study of the small Atlantic cod population in Gilbert Bay provides insight into intraspecific diversity in Atlantic cod populations (i.e. inshore populations), and the role population connectivity plays in that diversity. Specifically, it demonstrates how knowledge of dispersal, behaviour, and harvesting practices can be used to improve MPA effectiveness as a fisheries management tool.

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Appendix 1. DFO telephone survey questions to assess the effects of fishing season on harvesters in southern Labrador (see Chapter six).

| Questions asked to harvesters | Answer choices |
|---|---|
| Do you harvest cod commercially in the area surrounding William's Harbour (2Jm) or area between Salmon Point (52 38 N 55 44 W south) to Spear Point (52 27 N 55 37 W)? | A) Yes<br>B) No |
| Do you harvest cod recreationally in the area surrounding William's Harbour (2Jm) or area between Salmon Point (52 38 N 55 44 W south) to Spear Point (52 27 N 55 37 W)? | A) Yes<br>B) No |
| What time of year are cod fish typically most abundant in this area? (circle more than one answer if required) | a) July,<br>b) August,<br>c) August 15 to Sept 15,<br>d) September 7 to October 7,<br>e) Sept 15 to October 15 |
| What time of year are cod fish typically of best quality in this area? (circle more than one answer if required) | a) July,<br>b) August,<br>c) August 15 to Sept 15,<br>d) September 7 to October 7,<br>e) Sept 15 to October 15 |
| Would you expect to be negatively impacted if the commercial cod fishing season was regularly set for September 15 to October 15? | A) Yes<br>B) No |
| If yes, would you expect to be negatively impacted if the season was regularly set for September 7 to October 7? | A) Yes<br>B) No |
| What period would you prefer for the opening of the commercial cod fishery? | a) July,<br>b) August,<br>c) August 15 to Sept 15,<br>d) September 7 to October 7<br>e) Sept 15 to October 15 |
| Do you have any further questions or concerns about the Gilbert Bay Marine protected Area? | Commentary |